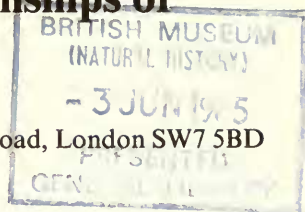


Notes on the anatomy and phyletic relationships of *Hemichromis* Peters, 1858

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Introduction

Students of cichlid taxonomy have long speculated on the phyletic relationships of the endemic African genus *Hemichromis* Peters (1858), a taxon which superficially appears quite distinct from other African cichlids, and in some respects is more like certain Neotropical members of the family.

Early views on the affinities of *Hemichromis*, albeit more probably statements of phenetic resemblance than phyletic affinity, are those of Pellegrin (1903: 252) and Sauvage (1907, 1910). Pellegrin considered *Hemichromis* to be close to, and differing little from, the South American genus *Acara* (probably to be interpreted as *Aequidens*); Sauvage, however, first allied *Hemichromis* with his fossil, *Palaeochromis*, from the Eocene of Africa, and later thought that genus to be intermediate between *Hemichromis* and *Acara*.

Entirely African affinities for the genus were implied by Regan (1922) who considered *Hemichromis* and *Haplochromis* (as then broadly conceived) to be very closely related.

There, at least in print, matters rested until fifty years later Loisel & Welcomme (1972) postulated *Hemichromis* as the nearest relative of their newly discovered genus *Thysia* from West Africa; these authors also suggested that *Hemichromis* might be an unnatural taxon, an idea apparently abandoned by the senior author a few years later (Loiselle, 1979). More recently, Van Couvering (1982) recognized *Hemichromis* as constituting the plesiomorph sister group of an assemblage comprising *Pseudocrenilabrus* and *Haplochromis*, the latter again broadly conceived as in Regan's time.

Only Loisel & Welcomme amongst these authors provided anything approaching a detailed reasoning for their conclusions. None based their views on a wide-ranging anatomical comparison with other taxa from Africa or those from the Neotropics. In fact, remarkably little is known about the anatomy of *Hemichromis*. The only source of information is Vandewalle's (1971:268–272) not especially detailed or widely comparative account of the cephalic skeleton and musculature in *H. fasciatus*.

One of the objects of the present paper is to take a fresh look at the phylogenetic relationship of *Hemichromis* using information derived from more detailed anatomical studies, by extending the comparative basis to include not only more African taxa but also Madagascan and Neotropical species, and by using, in the final analysis of its relationships, only features which, as far as can be established, are derived ones.

Another object of this paper is an attempt to assess whether or not *Hemichromis* should be ranked as one of the 'primitive' African cichlids, a status which it has been accorded by two recent workers, Cichocki (1976) and Van Couvering (1982).

The results of this investigation are, in one respect, disappointing. On the positive side, *Hemichromis* can be shown to be a member of the African cichlid assemblage, and that amongst that assemblage it is not an entirely primitive taxon; indeed it possesses several unique derived features, and shares many other apomorphies with various African and Neotropical species. The disappointment stems from the fact that a presumed sister group for the genus can only be recognized on a synapomorphy that could be considered equivocal.

Materials and methods

The entire collection of BMNH cichlid dry skeletons and alizarin preparations was examined. Thus, as far as African taxa are concerned a representative of virtually every genus was examined, and in the case of the larger lakes and rivers, several species of a genus were studied. In preparing the skeletal collections of Lake Victoria and Lake Edward haplochromines I had made notes on various anatomical features; these data were used in this paper, and so obviated the need for additional dissections. However, dissections were made on various taxa from Lakes Malawi, Tanganyika and Turkana, and on species from rivers and smaller water bodies. These are listed below.

Much of the information on Neotropical species was taken from Cichocki (1976), but several dry skeletons and alizarin preparations were examined, and dissections were carried out on others. These too are listed below, as are the various outgroup taxa studied.

The notation (1) or (2), which precedes non-*Hemichromis* species listed under the sections 'African material: Dissections' and in the Neotropical, Asian and Madagascan skeleton and dissected material sections, indicates the nature of the ethmopalatine articulation. (1) means a single, anterior articulation between the palatine and the lateral ethmoid; (2) indicates a double articulation: anteriorly as described above, and posteriorly between the palatine and a facet on the ventral face of the lateral ethmoid (see pp. 137–140).

Materials

Hemichromis fasciatus

Dissections: 1976.11.12:138–141; 1953.4.28:243–244.

Alizarin preparations: 1976.11.12:135–137; 1952.4.13:4218–4231.

Dry skeletons: 1953.4.28:243–248; 1883.4.19:15.

Hemichromis bimaculatus

Dissections: 1896.3.9:6–10

Alizarin preparations: 1982.4.13:4180–4186.

Dry skeletons: 1982.4.13:4180–4186; 1865.5.3:45.

The nature of the ethmopalatine joint, and the distribution of ethmomaxillary and ethmopalatine ligaments, in species other than *H. fasciatus* and *H. bimaculatus* were studied from dissections on:

H. guttatus 1906.5.28:66–67; *H. frempongi* 1917.4.20:27–28; 1942.12.30:1–10; *H. cerasogaster* 1979.3.5:358–9; 1899.11.27:67–86; *H. paynei* 1950.9.22:51–55; *H. elongatus* MRAC 172736–172750; *H. lifalili* AMNH 19704; *H. letourneauxi* 1907.12.2:2989–3013; *H. stellifer* AMNH 16864 (4 paratypes).

All *Hemichromis* specimens were chosen from material examined and identified by Loiselle (1979).

African species

Dissections:

- (2) *Astatotilapia flavijosephi* 1983.7.6:27–33
- (2) *Astatotilapia burtoni* 1950.4.1:2176–2200
- (2) *Astatotilapia 'bloyeti complex'* 1958.12.5:76–87
- (2) *Aulonocara nyassae* 1935.6.14:2251–2255
- (2) *Aulonocranus dewindti* 1969.9.30:4269–4641
- (2) *Bathybates fasciatus* 1960.9.30:6018–6020
- (1+2) *Bathybates ferox* 1960.9.30:5952–5957
- (1) *Bathybates graueri* 1960.9.30:6274–6283
- (2) *Bathybates horni* 1960.9.30:6284–6286
- (1) *Bathybates minor* 1950.4.1:5708–5744
- (1) *Bathybates vittatus* 1960.9.30:6293–6295
- (2) *Chilotilapia rhoadesi* 1935.6.14:2103–2112
- (2) *Chromidotilapia finleyi* 1979.2.23:18–19
- (2) *Chromidotilapia guentheri* 1973.5.14:615–626; 1930.3.24.25–26
- (2) *Corematodus shiranus* 1935.6.14:2008–2011
- (2) *Ctenochromis polli* 1964.5.28:1–2
- (2) *Cynotilapia afra* 1965.10.25:6–19
- (2) *Cyphotilapia frontosus* 1982.4.13:4737
- (2) *Cyrtocara eucinostomus* 1962.10.18:1–10
- (2) *Cyrtocara chrysonotus* 1935.6.14:1823–1832
- (2) *Eretmodus cyanostictus* 1950.4.1:5171–5183
- (2) *Genyochromis mento* 1965.10.26:24–29
- (2) *Gephyrochromis lawsi* 1956.9.4:18
- (2) *Grammatotria lemairei* 1950.4.1:3758–3785
- (2) *Hemibates stenosoma* 1961.11.22:999–1005
- (2) *Hemitilapia oxyrhynchus* 1936.5.14:2142–2145
- (1) *Konia dikume* 1973.5.14:643–649
- (2) *Labeotropheus fuelleborni* 1935.6.14:205–274
- (2) *Lamprologus cunningtoni* 1950.4.1:6677–6694
- (2) *Lamprologus moori* 1950.4.1:6586–6603
- (2) *Leptotilapia irvinea* 1974.1.2:225–228
- (2) *Lethrinops lethrinus* 1930.1.31:144–149
- (2) *Lichnochromis acuticeps* 1956.6.12:20–22
- (2) *Lobochilotes labiatus* 1950.4.1:616–639
- (1) *Myaka myaka* 1973.5.14:719–723
- (2) *Nanochromis nudiceps* unregistered ex Stanley Pool
- (2) *Oreochromis niloticus* 1907.12.2:3351–3353
- (2) *Oreochromis tanganyicae* 1919.1.16:126
- (2) *Oreochromis variabilis* 1958.12.4:1–7
- (2) *Pelmatochromis buettikoferi* 1911.5.31:45–48
- (2) *Pelmatochromis kribensis* 1952.8.26:7–8
- (2) *Pelvicachromis pulcher* 1915.4.13:45–47
- (2) *Pelvicachromis roloffii* 1972.9.27:78–85

- (2) *Petrotilapia tridentiger* 1965.10.26:30–36
- (2) *Pseudocrenilabrus philander dispersus* 1935.3.20:4–9
- (1) *Pterochromis congicus* 1901.12.21:77
- (2) *Pungu maclareni* 1973.5.14:769
- (2) *Rhamphochromis longiceps* 1935.6.14:2172
- (2) *Sarotherodon caroli* 1973.5.14:769
- (1) *Sarotherodon linelli* 1973.5.14:861–872
- (2) *Sarotherodon melanotheron* 1971.8.13:13–14
- (2) *Serranochromis angusticeps* 1932.12.16:538–540
- (2) *Steatocranus casuarius* 1977.1.11:274–410
- (2) *Stomatepia mariae* 1973.5.14:948–988
- (1) *Teleogramma gracilis* 1976.5.21:88–97
- (2) *Thoracochromis albertianus* 1929.1.24:318–322
- (2) *Thoracochromis buysi* unregistered. Cunene river
- (2) *Thoracochromis macconneli* 1973.11.13:38–58
- (2) *Thysia ansorgii* 1977.11.8:436–455
- (2) *Tilapia ruweti* 1969.3.28:1–6
- (2) *Tilapia sparrmani* 1966.7.20:12–13
- (2) *Trematocara unimaculatum* 1961.11.22:529–537
- (2) *Tristramella simonis* 1968.12.13:55–65
- (2) *Xenotilapia melanogenys* 1950.4.1:3944–3978

Genus *incertae sedis*:

- (2) *Pelmatochromis thomasi* 1914.12.9:9–11 (syntypes); 1981.8.17:22–41; 1981.6.19:119–121

Madagascan and Asian species

Dissections;

- (2) *Ptychochromis oligacanthus* 1980.2.1:5–6; 1982.2.25:71–73
- (1) *Paratilapia polleni* 1876.10.3:33; 1960.9.30:6274–6283
- (1) *Paretroplus dami* 1969.2.7:1–3
- (1) *Etroplus maculatus* 1958.6.10:69–74

Neotropical species

Dissections:

- (2) *Acarichthys heckeli* 1925.10.28:398–402
- (2) *Aequidens vittatus* 1973.2.7:1–9
- (2) *Astronotus ocellatus* 1926.10.27:440–443
- (1) *Batrachops reticulatus* 1968.9.26:327–328
- (1) *Chaetobranchius flavescens* 1926.10.27:426–427
- (1) *Cichla ocellaris* 1968.9.26:23–24
- (1) *Cichlasoma motaguense* 1925.3.6:132–135
- (2) *Crenicichla saxatilis* 1981.6.9:1209–1210
- (1) *Heterotilapia multispinosa* 1925.3.6:162–164
- (1) *Microgeophagus ramirezi* 1952.7.30:6–7
- (1) *Pterophyllum scalare* unregistered ex Zoo. Soc. London

Dry skeletons:

- (1) *Acaronia nassa*
- (1) *Aequidens tetramerus*
- (1) *Cichla ocellaris*
- (2) *Cichlasoma cyanoguttatum*
- (1) *Cichlasoma facetum*
- (1) *Cichlasoma motaguense*
- (1) *Cichlasoma sieboldi*
- (2) *Crenicichla johanna*
- (1) *Geophagus braziliensis*
- (1) *Geophagus jurupari*
- (1) *Geophagus surinamensis*
- (1) *Symphysodon discus*

Outgroups

Dissections:

Centropomidae: *Lates niloticus*., UnregisteredSerranidae: *Serranus cabrilla* 1936.12.30:7–8Percidae: *Perca fluviatilis* 1967.8.3:21–25Labridae: *Halichoeres bivittatus* 1980.9.22:250–252*Pseudolabrus luculentus* 1977.4.4:101–108Pomacentridae: *Amphiprion ocellaris* 1984.1.18:185–187*Pomacentrus leucostictus* 1933.10.12.41–50Embiotocidae: *Cymatogaster aggregata* 1981.5.19:45–69*Embiotoca jacksoni* 1981.5.19:5–6*Neoditrema nansonnelli* 1905.2.4:240–244**Abbreviations used in text figures**

The scale bar in the figures is divided into millimetres.

A_{1-3}	Adductor mandibulae muscles 1–3
A_w	Adductor mandibulae muscle A_w
af hymd	Anterior facet for head of hyomandibula
ang art	Anguloarticular bone
apn	Aponeurosis
art s pb3	Articular surface of 3rd pharyngobranchial bone
art v lat pr	Surface for articulation with lateral process of the vomer
awn	Lateral awning area
bb 1–4	1st–4th basibranchial elements (4th is cartilaginous)
bh	Basihyal bone
boc	Basioccipital
boc f	Basioccipital facet for articulation with upper pharyngeal bones
bsph	Basisphenoid
cal	Calyx
cb 1–4	1st–4th ceratobranchials
cl	Cleithrum
cor	Coracoid
cts	Connective tissue sheet
d cart	Dorsal accessory cartilage
den	Dentary
ect	Ectopterygoid
entp	Entopterygoid
epo	Epioccipital
epb 1–4	1st–4th epibranchials
epb 4 br	Bony ridge on 4th epibranchial
exo	Exoccipital
f hym	Foramen for branch of facial nerve
f oln	Foramen for olfactory nerve
fr	Frontal
fz	Frayed zone
ga II–IV	Gill arches I–IV
hb 1–3	1st–3rd hypobranchials
hym	Hyomandibula
hymd sh	Hyomandibulad pit
hypp	Hypurapophysis
ic	Intercalar
inth	Interhyal
iop	Interoperculum

lac fac	Facet for lachrymal (1st infraorbital) bone
lat comm	Lateral commissure
lat pr vom	Lateral process of vomer
l eth	Lateral ethmoid
lphyj	Lower pharyngeal bone
<i>m aap</i>	Adductor arcus palatini muscle
<i>m add op</i>	Adductor operculi muscle
<i>m add 5</i>	Adductor 5 muscle
<i>m c-p²</i>	Cranio-pharyngobranchialis 2 muscle
<i>m dilop</i>	Dilatator operculi muscle
<i>m im</i>	Intermandibularis muscle
<i>m lap</i>	Levator arcus palatini muscle
<i>m le 1-4</i>	Levator externus muscle 1-4
<i>m lev post</i>	Levator posterior muscle
<i>m li 1&2</i>	Levator internus muscles 1 & 2
<i>m lop</i>	Levator operculi muscles
<i>m obl d ant</i>	Obliquus dorsalis anterior muscle
<i>m obl d post¹</i>	Obliquus dorsalis posterior muscle, pars medialis
<i>m obl d post²</i>	Obliquus dorsalis posterior muscle, pars lateralis
<i>m pro pect</i>	Protractor pectoralis muscle
<i>m rab</i>	Retractor arcuum branchialium muscle
<i>m sph oes</i>	Sphincter oesophagi muscles
<i>m tdp</i>	Transversus dorsalis posterior muscle
<i>m t-e2</i>	Transversus epibranchialis 2 muscle
max	Maxilla
meth	Mesethmoid
metp	Metapterygoid
metp r	Ridge on metapterygoid
mxhd	Maxillary head of palatine bone
ncc	Neurocranial condyle of premaxilla
oes	Oesophagus
op	Operculum
pal	Palatine
pal-lac lig	Palato-lachrymal ligament (cut)
pal-pal lig	Palato-palatine ligament
pal-vom lig	Palato-vomerine ligament
pal vom pr	Vomerine process of palatine
par	Parietal
pc 1-2	First and second postcleithra
p f hymd	Posterior facet for head of hyomandibula
phyb 1-3	Pharyngobranchials 1-3
pop	Preoperculum
pop-retar lig	Preopercular-retroarticular ligament
pr	Anterior process on 2nd postcleithrum
pro	Prootic
psph	Parasphenoid
psph f	Parasphenoid facet for articulation with upper pharyngeal bones
pto	Pterotic
pts	Pterosphenoid
q	Quadrate
qr r	Quadrangular region of 4th epibranchial bone
ra	Retroarticular
r cart	Rostral cartilage
rdg	Ridge
rds	Pectoral fin radials

r ect	Recess in ectopterygoid bone for the <i>adductor arcus palatini</i> muscle
rost f	Rostral fenestra
r pal	Recess in palatine bone for the <i>adductor arcus palatini</i> muscles
sc	Scapula
sdl	Saddle
shr	Shank ridge
soc	Supraoccipital
socc	Supraoccipital crest
sop	Suboperculum
sp	Shank spine on 4th epibranchial bone
sph	Sphenotic
sut	Suture between anterior flange of hyomandibula and metapterygoid
symp	Symplectic
t A_1a	Tendon from muscle A_1 to maxilla
t A_1b	Tendon from muscle A_1 to lower jaw
t A_w	Tendon from muscle A_w
tem	Triangular prominence on maxilla
t-1 pal proc	Thumb-like process of palatine (for articulation with anterior face of lateral ethmoid)
trf	Triangular fossa in frontals
up 4	4th upper pharyngeal tooth plate
v cart	Ventral accessory cartilage
vom	Vomer
vom c	Vomerine crest
vom fs	Vomerine fossa
vp pal	Vomerine process of palatine

Notes on the osteology and anatomy of *Hemichromis*

Apart from certain features studied by Cichocki (1976), and a few neurocranial characters noted by Stiassny (1982) and Van Couvering (1982), the only osteological and myological account of *Hemichromis* is that of Vandewalle (1971). That account is somewhat superficial, took into account only *H. fasciatus*, and overlooked most of the major anatomical peculiarities of the genus.

The anatomical and osteological descriptions given below are also based primarily on *H. fasciatus*, type species of the genus. They are, however, supplemented by observations on *H. bimaculatus*, and where material permitted, on other species of the genus as well. One critical feature, the nature of the palatoethmoidal articulation, has been checked in ten of the species recognized by Loisel (1979) in his species-level revision of the genus. No suitable material of *H. cristatus* was available for dissection, but the palatoethmoidal articulation in this species was checked, and confirmed, from radiographs.

Osteology

NEUROCRANIUM

The overall morphology of the neurocranium is shown in Figs 1 & 2, and calls for no further comments.

Ethmovomerine region (Figs 1 & 2). This region of the skull departs markedly from the condition found in all other cichlids examined. In large part these peculiarities are associated with the unusual and unique ethmopalatine articulatory system of *Hemichromis* (see pp 138–140). Since that system occurs in all species, most of the peculiarities occurring in this region of the skull in *H. fasciatus* and *H. bimaculatus* are probably present in every member of the genus.

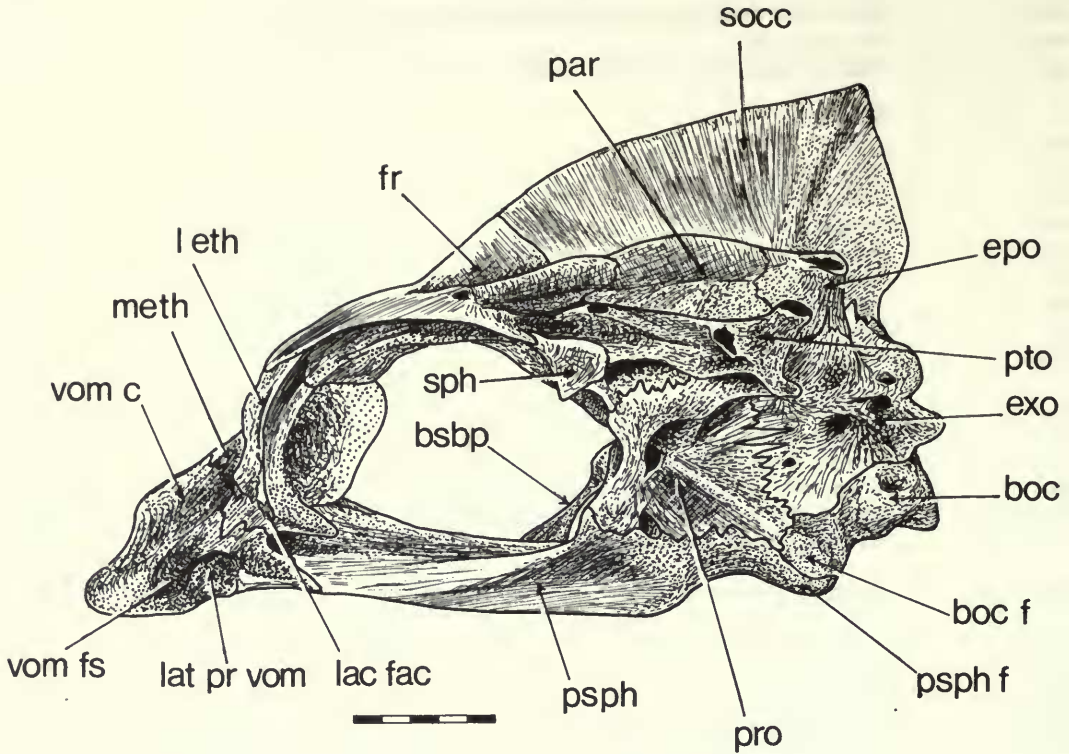


Fig. 1 *Hemichromis fasciatus*. Neurocranium, left lateral view (1953.4.28:243-4; 120 mm SL).

Over slightly more than the posterior half of its length, the dorsal surface of the vomer in *H. fasciatus* is considerably elevated to form a casket-like crest with a broad, slightly cambered upper surface. The crest is continuous with a similar median elevation of the mesethmoid's anterior half. The mesethmoid and the vomer have a deeply interdigitating sutural union. Immediately anterior to the suture, at least in dry skulls, a small area of the vomer's dorsal surface is incomplete (the rostral fenestra of Stiassny, 1981a:73). In freshly prepared skulls this ovoid hole is filled by a protruding cartilaginous plug.

A similar ethmovomerine crest is present in *H. bimaculatus*, but is relatively lower and less obvious than its counterpart in *H. fasciatus*.

In both species the tip of the vomer is bulbous and indented medially. A short distance behind the bulbous region, the ventrolateral margin of the vomer is produced, on each side, into a broad, near-triangular lateral process whose tip projects slightly beyond the lateral margins of the bulbous part (Figs 1-4). The anterior surface of the lateral process underlies, and articulates with, the vomerine process of the palatine (see p. 144; also Fig. 4). The gently rounded dorsal and posterior faces of the lateral process contact the ventral face of the palatine immediately behind the base of that bone's vomerine process.

As far as I can tell from an extensive survey of African and Neotropical cichlids, *Hemichromis* is unique in having this kind of vomerine support for, and articulation with, the palatine. In all other taxa the only vomeropalatine contact is through a simple, face-to-face joint between the articular head of the palatine's vomerine process (the palatine wing of Barel *et al.*, 1976) and a facet on the lateral aspect of the vomer (the vomerine palatinad articulation of Barel *et al.* 1976).

Hemichromis fasciatus and *H. bimaculatus* do, however, have a second point of articulation between the vomer and palatine which is apparently homologous with the usual one in cichlids. It is effected through the tip of a well-developed process on the palatine inserting into a deep pit in the lateral wall of the vomer immediately above the base of the lateral vomerine process (see

above). The pit in *Hemichromis* would seem to correspond to the vomerine fossa in other cichlids (see Stiassny, 1981a), and the process on the palatine with the palatine wing (*sensu* Barel *et al.*, 1976). The most obvious difference between the two systems is that, in other cichlids, the vomerine palatinad articulation of Barel *et al.* lies immediately anterior to the vomerine fossa, whereas in *Hemichromis* the articulation point lies within what appears to be the vomerine fossa.

All the cichlids I examined, apart from *Hemichromis*, have an articulation anteriorly between the lateral ethmoid and the palatine. Usually this is brought about by contact between a facet on the medial face of the palatine meeting a facet on the lateral aspect of the lateral ethmoid, near or overlapping its suture with the vomer (*ie* Stiassny's [1981a] ovoid fenestra; see also figs 1–3 in that paper). No such articulation occurs in any of the *Hemichromis* species I examined. Instead, there is an elaborate joint developed between the anterior face of the lateral ethmoid and the palatine; this will be described below.

In addition to the anterior contact between the lateral ethmoid and the palatine, there is, in the great majority of African cichlids examined, and in some but relatively fewer Neotropical species, a posterior ethmopalatine articulation as well (see lists in 'Materials' section, p. 132; also Cichocki, 1976). This posterior contact is between a short, drum-like facet on the ventral surface of the lateral ethmoid, and an elongate facet on the postero-dorsal surface of the palatine's posterior wing (the lateral ethmoid articulation facet of Barel *et al.*, 1976). Generally the drum-like facet on the lateral ethmoid is situated near the posterior and median margins of that bone. No such posterior ethmopalatine articulation is present in *Hemichromis*, and there is no drum-like facet ventrally on the lateral ethmoid. Indeed, there is a relatively large gap between the palatine and that region of the skull.

Hemichromis does, however, have a different kind of ethmopalatine articulation, and one which has not been found in any other cichlid. The articulation (see Figs 3 & 4) is between an upwardly directed, transversely orientated process on the palatine (probably corresponding to Barel *et al.*'s [1976] mesethmoidal process in *Astatotilapia elegans*) and the anterior face of the lateral ethmoid immediately below the foramen for the olfactory nerve (see Fig. 4). The lateral ethmoid facet has a complex form. Anteroventrally there is a well-defined, vertically aligned articular surface for the palatine process. Its rounded anterior face runs laterally almost at right angles to the skull's sagittal plane and extends from about the level of the ethmovomerine crest to the point where the lateral ethmoid is produced downwards to form the prefrontal margin of the orbit. Immediately behind this part of the facet the ethmoid is formed into a second, but horizontally aligned articular surface. It lies in the floor of a deep and broad pit on the posterior wall of which the foramen for the olfactory nerve is situated. The medial wall of the pit is formed by the mesethmoid, but its floor, lateral wall and posterior face are formed by the lateral ethmoid. This facet, too, is involved in articulation with the palatine process (see p. 143 below).

There are some slight interspecific differences in the morphology of the ethmopalatine articulation in *Hemichromis*. The ethmoid pit and its articular surfaces are, however, always present but, as in *H. bimaculatus*, the horizontal component of the ethmoid facet may be better defined than the vertical one.

Neither *H. fasciatus* nor *H. bimaculatus* has an ovoid fenestra (see above). This cartilage-filled gap between the lateral ethmoid and the vomer was somewhat more accurately designated by Barel *et al.* (1976) as the mesethmoid-palatine facet, since it serves, in the majority of cichlids, as the anterior point of articulation between the palatine and the ethmoid (or ethmovomerine bloc if the facet, as it often does, spans part of the suture between the vomer and lateral ethmoid).

That the facet (or fenestra) has disappeared in *Hemichromis* is not surprising when one considers the single type of ethmopalatine articulation present in that genus (see above, p. 137).

In short, *Hemichromis* differs from all other cichlids in having a double (and complex) palatovomerine articulation, and in having an elaborate articulation between the palatine and the anterior face of the lateral ethmoid. In other taxa this joint is a simple one between the palatine and the lateral ethmoid, or lateral ethmoid-vomer junction region. *Hemichromis* does, however, share with a number of other cichlids, especially Neotropical taxa, the loss of contact and hence articulation between the ventral face of the lateral ethmoid and the posterior wing of the palatine (see p. 166 for further discussion).

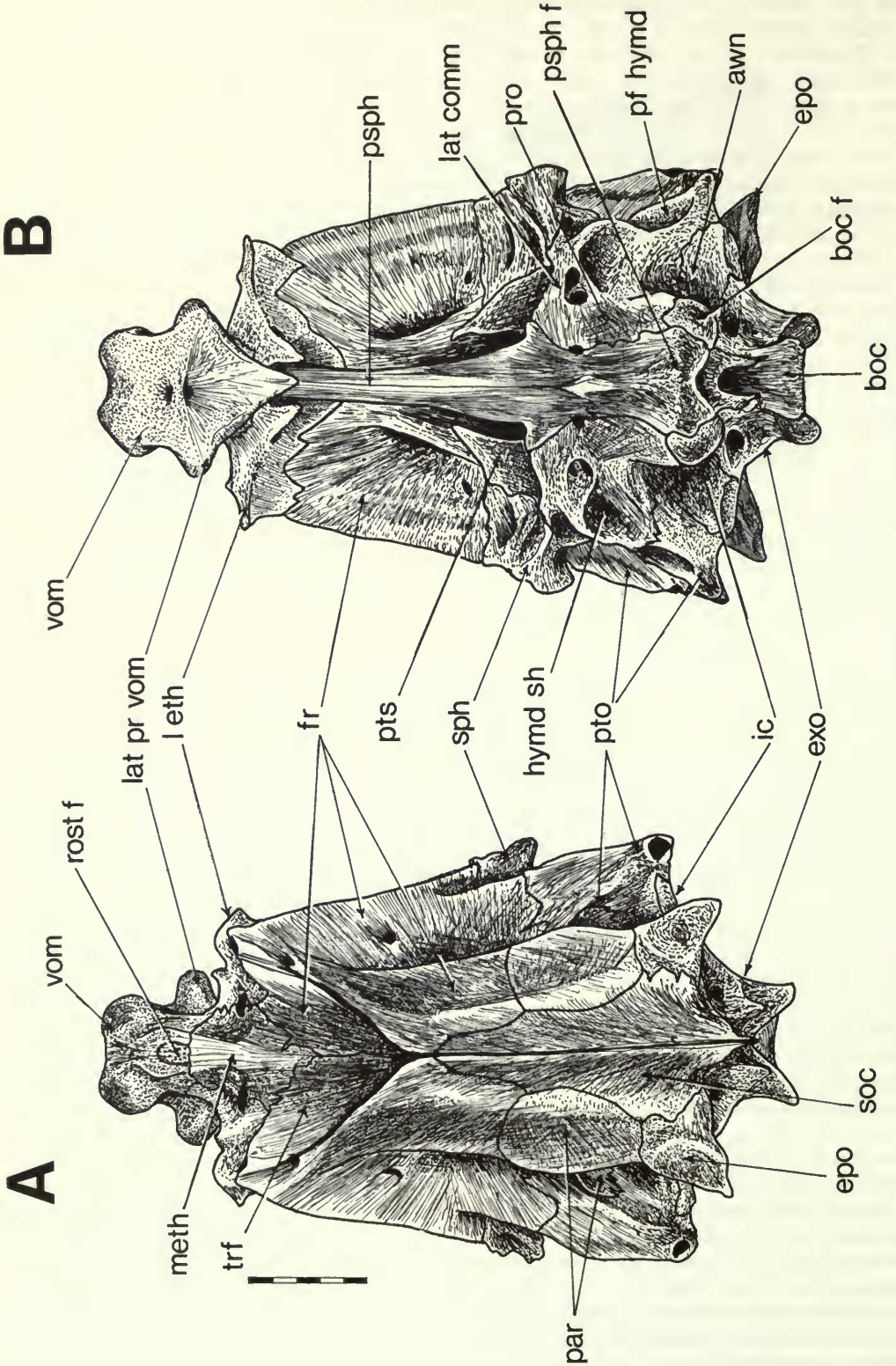


Fig. 2 *Hemichromis fasciatus*. Neurocranium in: A. Dorsal view. B. Ventral view (1953.4.28: 243-4).

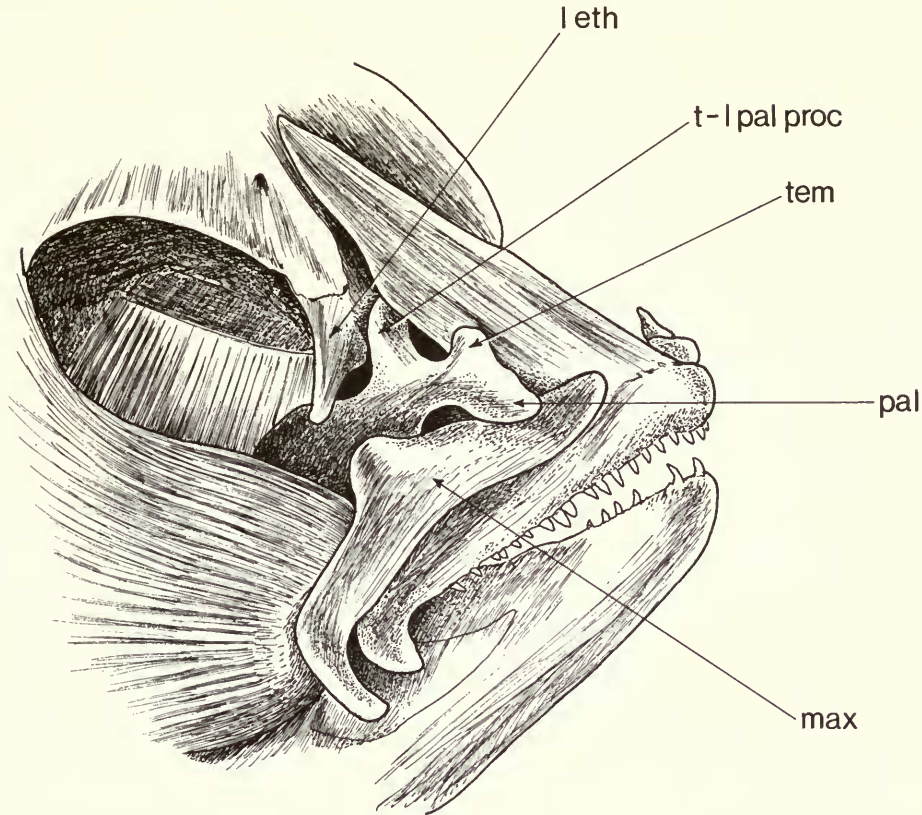


Fig. 3 *Hemichromis fasciatus*. Dissected snout, in dorso-anterior view, to show palato-ethmoid articulation.

Dorsicranium (Fig. 2A). As Vandewalle (1971) noted in *H. fasciatus*, there is a large, cartilage-filled area in the floor of the post-temporal fossa. It extends between the inner margins of the parietal, epioccipital and pterotic bones forming the fossa. Such a cartilage area, but of variable extent is present in all the cichlids I examined.

In *H. fasciatus* the mesethmoid and frontals meet along a broad, shallowly curved front which is continued laterally by the smooth overlap of lateral ethmoids and frontals. The fossa-like area lying between the anterior continuation of the frontals is broad and triangular, its apex is directed posteriorly, and it is deeply scoop-shaped in transverse section. The floor and walls of this triangular fossa (Fig. 2A) are formed by the frontals. Posteriorly its median wall is not continued backwards, as is usual in cichlids, as a pair of roofed, almost tubular cavities. These cavities are, however, present in *H. bimaculatus*. It would seem that the condition in *H. fasciatus* has resulted from the frontals failing to develop the medially directed and horizontal flanges which in other taxa, including *H. bimaculatus*, roof the median posterior extension of the fossa.

Vandewalle (1971) does not mention the absence of roofed extensions to the frontal fossa in *Hemichromis fasciatus*, but he does comment '... comme le signale Boulenger (1901), la crête supraoccipitale d'*Hemichromis* est *bifurquée* entre les orbites pour recevoir le processus ascendant des premaxillaire, ...' [italics added].

Boulenger's original observation and Vandewalle's confirmation of it are puzzling because neither the supraoccipital nor its crest extend anteriorly as far as the distal tips of the premaxillary ascending processes. I suspect that both authors misidentified, as part of the supraoccipital, the oblique, mediolaterally directed crests developed above the anterior part of the supraorbital lateral-line tubule on each frontal. These crests meet in the midline at the anterior tip of the

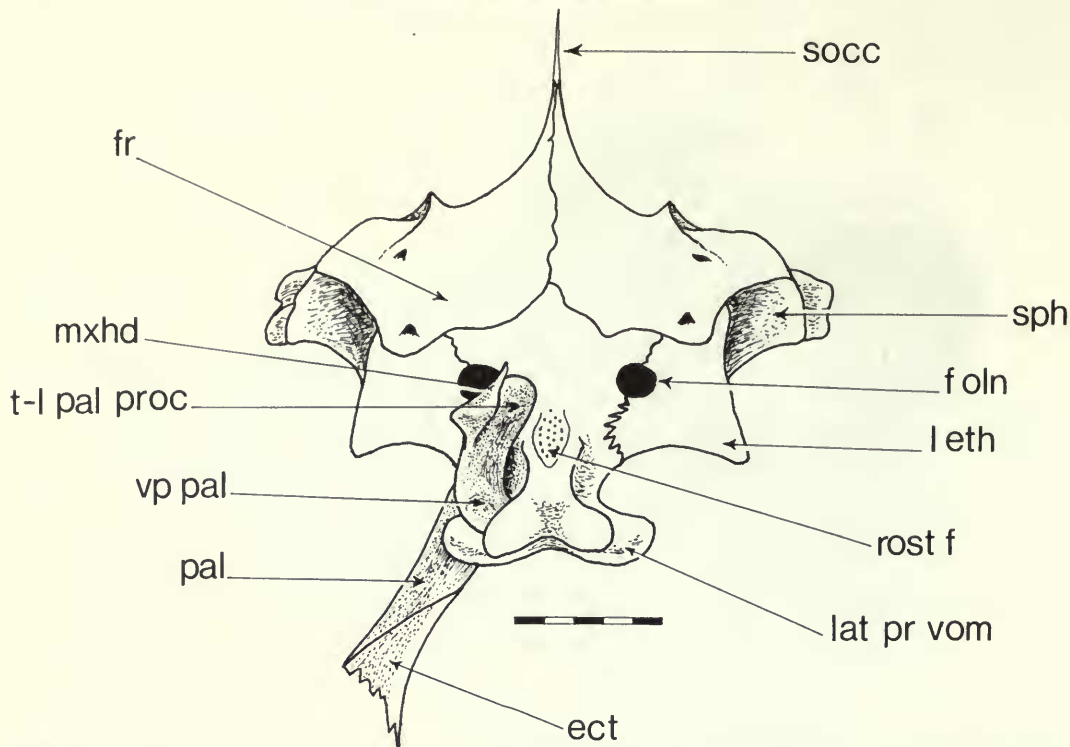


Fig. 4 *Hemichromis fasciatus*. Frontal view of neurocranium with right palatine in articulation, to show support of palatine by lateral process of vomer, and articulation of the thumb-like palatine process with the lateral ethmoid. (1953.4.28:243-4).

supraoccipital bone above the single coronal pore, and delimit the posterior margin of the scoop-like frontal fossa described earlier (Fig. 2A). The crests are homologues of the upswept anterior margin of the frontal area which, in other cichlids, roof the fossa's tunnel-like posterior extensions. Presumably it is the medial union of the crests anterior to the supraoccipital, and their apparent continuity with that bone, which misled Boulenger and Vandewalle into describing a bifurcate supraoccipital in *H. fasciatus*.

Otic region. The *pars jugularis* and *lateral commissure* are of the modal perciform type (Fig. 5). Van Couvering's figure (1982: fig. 5) of the *pars jugularis* in *H. bimaculatus* is slightly misleading since its posterior opening seems to be directed posteroventrally and not, as it actually is, posteriorly; this discrepancy probably is a result of the way (unspecified) in which the specimen was orientated.

A most noticeable departure of *Hemichromis* from the modal cichlid condition is seen in that part of the otic skull which Barel *et al* (1976) term the *hyomandibulad shell*. The hyomandibulad shell is that ventrally facing region of the prootic from which the greater part of the *levatoris externi* muscles of the gill arches originates. In all cichlids I have examined, apart from *Hemichromis*, the shell is a flat or weakly concave area. In *Hemichromis*, however, it is a deep, dorsally directed indentation (Figs 1, 2 & 5) which, when seen from below, resembles a pyramidal pit. As far as I can tell, a deep, pit-like hyomandibulad shell is unique to *Hemichromis* amongst the cichlids, and does not occur elsewhere outside the family.

Immediately behind the pit, the area formed by the meeting of the pterotic, prootic, intercalar and exoccipital bones (Figs 2 & 5) was designated as the *lateral awning* by Barel *et al* (1976). In *Hemichromis*, especially in *H. fasciatus*, the awning is much more deeply concave than it is in other cichlids. Like the hyomandibulad pit, the lateral awning in *Hemichromis* is approximately triangular in outline and pyramidal in form. It is, however, a less distinctive departure from the

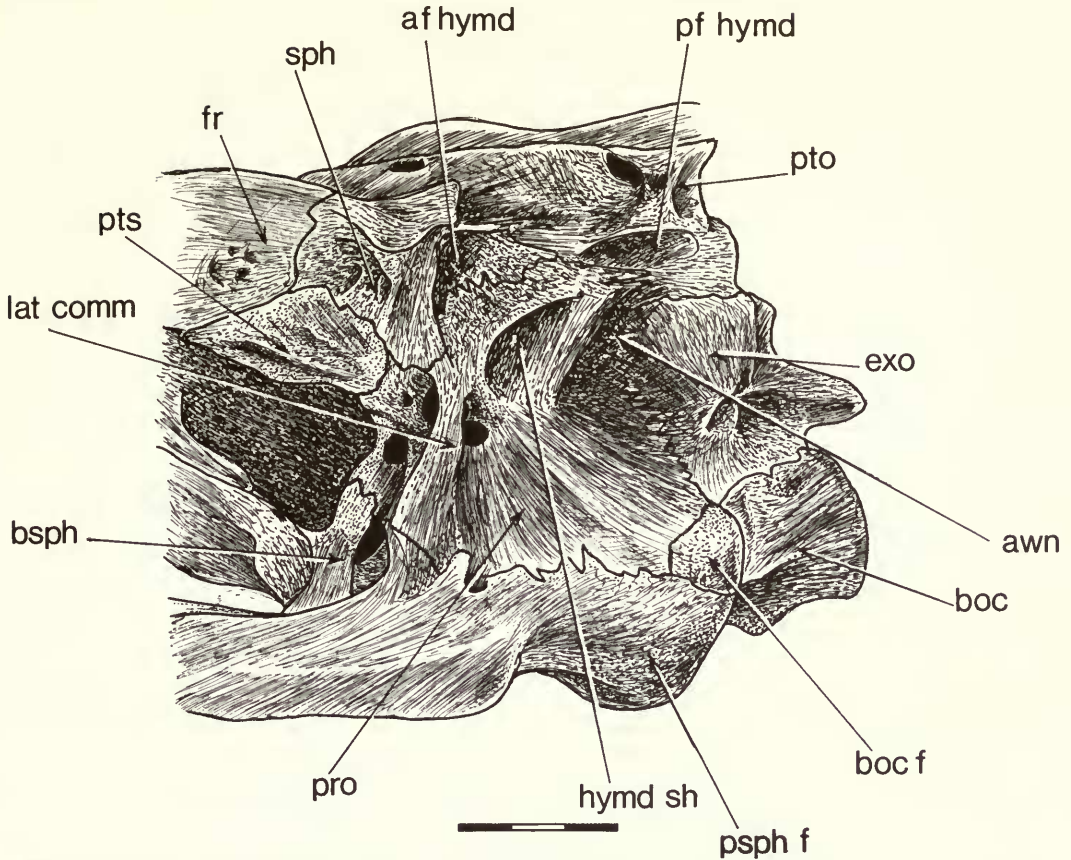


Fig. 5 *Hemichromis fasciatus*. Otic region of skull (left side) to show *pars jugularis* and its lateral commissure, and the form of the neurocranial apophysis for the upper pharyngeal bones. Specimen viewed from above and somewhat anteriorly, the transverse axis of the skull rotated to the right through *ca* 130° (1953.4.28:243–4).

usual cichlid condition, and is approached by the awning in, amongst other African species, *Pelmatochromis* and *Chromidotilapia*, and by the awning in some Neotropical taxa as well.

The intercalar is a large bone occupying somewhat more than the posterior half of the roof of the awning area.

Neurocranial apophysis for the upper pharyngeal bones. Structurally, the apophysis in *Hemichromis* is of the *Haplochromis*-type (Regan, 1920; also discussion in Greenwood, 1978), with a substantial basioccipital contribution on each side (Figs 1 & 5).

When the skull of *H. fasciatus* is viewed from behind, the ventral face of the apophysis is markedly convex, with most of its surface sloping upwards and outwards at an angle of about 45° to the horizontal. In sharp contrast, when the skull of *H. bimaculatus* is viewed in this way the apophyseal surface is virtually horizontal and thus like the modal condition in cichlids with a *Haplochromis*-type apophysis.

SUSPENSORIUM (Figs 6–8)

Palatoquadrate arch (Figs 6 & 7). Not surprisingly, in view of the unusual ethmopalatine articulation in *Hemichromis*, the *palatine* itself has a very characteristic form.

In *H. fasciatus* the bone is stout, with a short and wide maxillary process whose dorsomedial margin is produced into a wide-based triangular prominence. A little behind that prominence

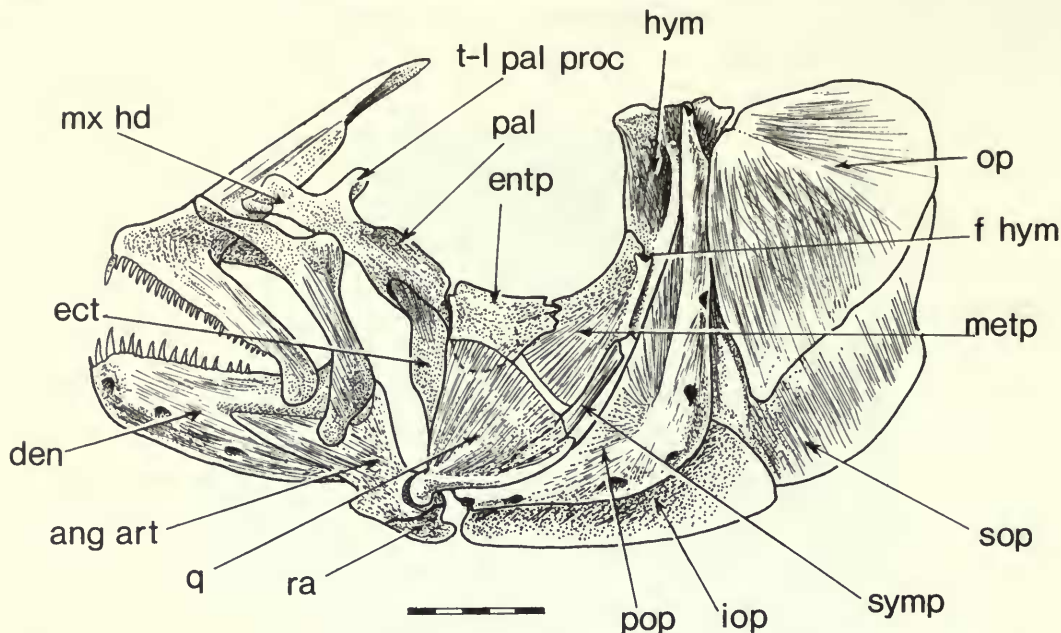


Fig. 6 *Hemichromis fasciatus*. Suspensorium, jaw elements and opercular series of the left side, in lateral view. The rostral cartilage has been removed (1976.11.12:135-7).

there is a stout, thumb-like, dorsally directed projection sloping backwards at a slight angle (Figs 3 & 7); it is this process which articulates with the compound facet on the anterior face of the lateral ethmoid (see p. 139). In frontal view the process is noticeably broadened over its distal half, and has a broadly rounded dorsal margin (Fig. 4). The posterior face and dorsal margin of this broadened region have the smooth appearance typical of articular surfaces. It is these areas which contact the facets of the lateral ethmoid. When the palatoquadrate arch is *in situ*, the rounded margin of the process lies just below the lower rim of the olfactory nerve foramen (Fig. 4). At the base of the process there is an ill-defined, low, anteromedially directed boss to which the palato-palatine ligament is attached (see p. 158).

The thumb-like process in *Hemichromis* is apparently the homologue of the low, transversely aligned mesethmoid process (*sensu* Barel *et al*, 1976) on the palatine of other cichlids.

The so-called lateral ethmoidal facet (Barel *et al*, 1976) which, in other cichlids, occupies the greater part of the palatine's dorsal margin posterior to the mesethmoidal process, is not developed in *Hemichromis*. Instead, this margin of the bone is produced into a low and thin flange delimiting an elongate depression on the medial face of the palatine (Fig. 21). This depression accommodates, in part, the palatine extension of the *adductor arcus palatini* muscle (see p. 156), and in part the head of the ectopterygoid.

On the palatine's medial face, very slightly behind the base of the thumb-like process, there is a stout and flat vomerine process (the palatine wing of Barel *et al*, 1976). The very clearly demarcated projection is directed ventromedially; its flattened posterior face articulates with the upper surface of the lateral process of the vomer (see p. 138).

For a short distance behind the origin of the vomerine process the ventral margin of the palatine is slightly excavated, the excavated part having a gently rounded margin which lies over the somewhat convex posterior face of the lateral process on the vomer (see p. 138).

The palatine in *H. bimaculatus* is more slender and far less robust than is the palatine of *H. fasciatus*. Otherwise, however, the bones in the two species show all the same characteristic features, except that the triangular prominence is very low and barely differentiated in *H. bimaculatus*.

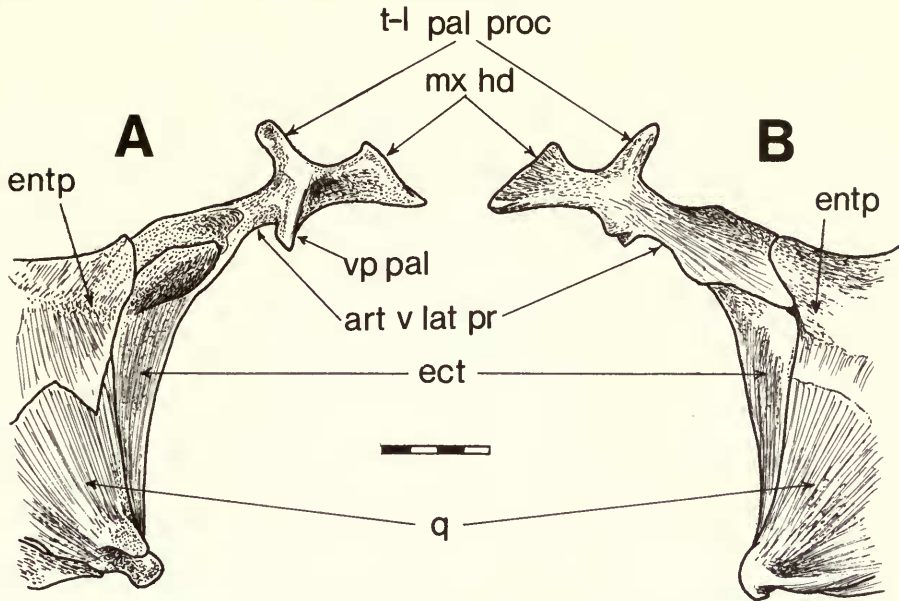


Fig. 7 *Hemichromis fasciatus*. Palatine and ectopterygoid, with entopterygoid in part. A. Medial aspect. B. Lateral aspect. (1953.4.28:243-4).

Posterodorsally, the *metapterygoid* in both species is in intimate contact with the ventral margin of the anterior flange of the hyomandibula, but no interdigitating suture is developed between the two bones (Fig. 6).

In the great majority of African cichlids examined (including *Pelmatochromis* and *Chromidotilapia*) as well as in several Neotropical taxa, the metapterygoid and the hyomandibular flange are not in contact or even closely apposed to one another. In some Neotropical species (eg *Cichla*) however, there is an extensive interdigitating suture between the bones (see Fig. 8). Unfortunately, much of the dry skeletal material of Neotropical species available to me is damaged in this part of the palatoquadrate arch, making it difficult to assess the modal condition in these fishes.

Amongst the so-called etropline cichlids (see Cichocki, 1976) which I could examine (*Eetroplus suratensis* and *E. maculatus* [both Asian species], and *Paratilapia polleni*, *Ptychochromis oligacanthus* and *Paretroplus polyactis* [all Madagascan]), there is an intimate appositional or sutural contact between the metapterygoid and the hyomandibula's anterior flange. However, Van Couvering (1982: fig. 7c) illustrates a specimen of *Eetroplus maculatus* (BMNH:659) in which there is no contact between these parts of the bones. Regrettably, this specimen is now extensively damaged and so it cannot be checked against Van Couvering's figure. In an alizarin preparation of this species, made from a specimen *ca* 33 mm standard length (BMNH 1889.2.1:3877-3881) the posterodorsal margin of the metapterygoid closely approaches the anterior flange of the hyomandibula, but does not contact it, thus resembling the situation figured by Van Couvering. In sharp contrast there is a distinct, albeit short, sutural union between the bones in a larger specimen, *ca* 50 mm standard length (alizarin prep., BMNH 1958.6.10: 68-74). These specimens would suggest, therefore, that the nature of the contact, or the lack of contact, is related to the fish's size. Thus it is important to note that all the other etropline material I examined (see above) was from specimens much larger than 50 mm standard length.

Judging from the outgroup taxa examined, and from descriptions in the literature, sutural contact between the anterior flange of the hyomandibula and the metapterygoid, or merely direct contact between them, is the plesiomorphic state (Johnson, 1980; see also Van Couvering, 1982).

In *Hemichromis no calyx* (see Barel *et al*, 1976:199; fig. 14A; also Fig. 8) is developed between

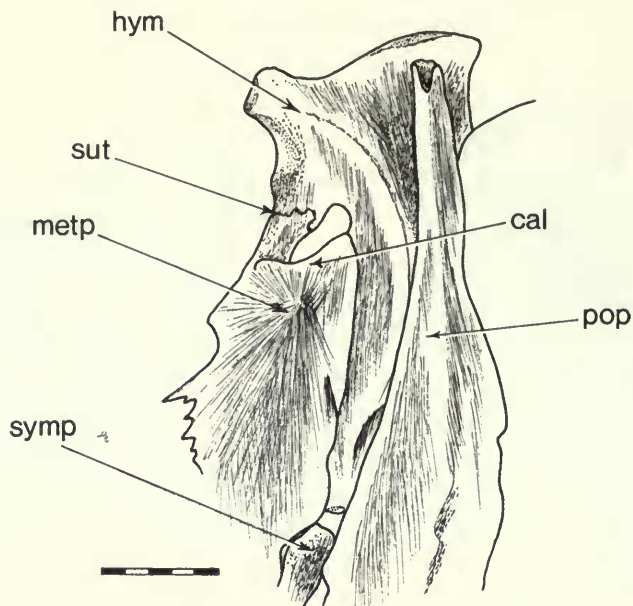


Fig. 8 *Cichla ocellaris*. Left metapterygoid and hyomandibula, in lateral view, to show the bones' sutural union, and the calyx (1895.3.29:30).

the metapterygoid and the hyomandibula. The majority of African taxa (including *Pelmatochromis*, *Pelvicachromis* and *Chromidotilapia*) have a well-developed calyx of the type described by Barel *et al* (*op. cit.*, *loc. cit.*) in *Astatotilapia elegans*. In some species, however, the calyx's medioposterior wall, otherwise formed from either or both the metapterygoid and, or, the hyomandibular shank, is very poorly developed. Thus, in these species the calyx has only an anterior wall, derived from a circumscribed, anterolateral outpocketing on the posterodorsal face of the metapterygoid.

The calyx is absent in some Neotropical species (eg *Petenia splendida*), greatly reduced in others, and is present in either its completely or incompletely backed state (eg *Cichla*) in yet others. Its dorsal opening also shows a continuous size gradient, from small to expansive.

In all the etroplines examined (see above) a calyx is present and open-backed like that in *Cichla* (Fig. 8), and its dorsal opening ranges from small to large.

The presence of a calyx or calyx-like structure would seem to be a plesiomorphic feature amongst percoids (see Johnson, 1980; pers. observations). Its loss in certain cichlid taxa, including *Hemichromis*, could thus be interpreted as a derived condition. The distribution pattern of this apomorphy within the Cichlidae, however, renders it likely that the calyx has been lost independently on several occasions within Neotropical lineages of the family but, apparently, only once in Africa, namely in *Hemichromis*. Developmentally a calyx could be associated with a shift in the insertion of the *levator arcus palatini* muscle, which thereby prevents the formation of close contact between the anterior flange of the hyomandibula and the greater part of the metapterygoid's posterodorsal border.

Hyomandibula. The anterior flange is well-developed in both *H. fasciatus* and *H. bimaculatus* (Fig. 6). The shank of the bone is about two-thirds as long as the distance between the surface of the two articular heads and a line drawn horizontally through the ventral margin of the anterior flange.

Other elements of the suspensorium are illustrated in Fig. 6 and require no further comment except to note that there is no palato-entopterygoid gap, and that in the largest skeleton of *H. fasciatus* examined the posterior margin of the palatine is excavated to receive the anterior tip of the entopterygoid; in smaller specimens the two bones are merely apposed to one another (Fig. 21).

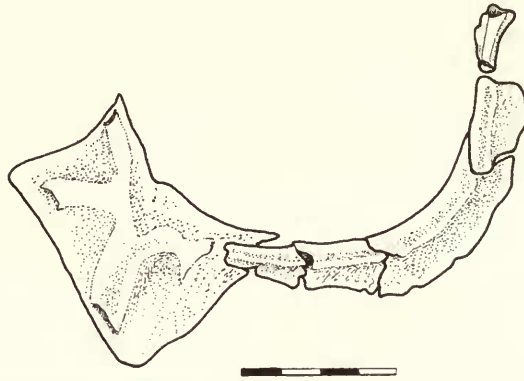


Fig. 9 *Hemichromis fasciatus*. Infraorbital bones, left side, in lateral view (1976.11.12:135-7).

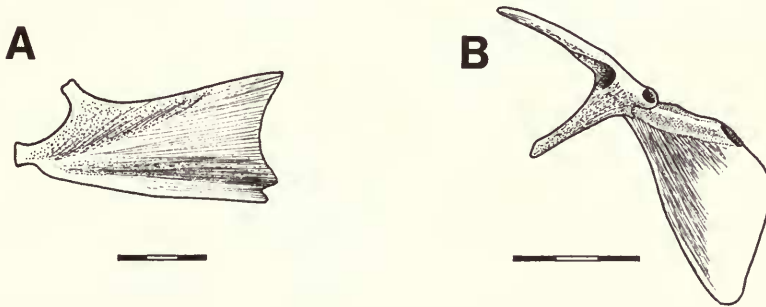


Fig. 10 *Hemichromis fasciatus*. A. Urohyal, in left lateral view. B. Left supracleithrum and posttemporal bones in articulation; lateral view (1976.11.12:135-7).

INFRAORBITAL BONES (Fig. 9)

These bones in *H. fasciatus* are illustrated in Fig. 9. According to Vandewalle (1971) there are, excluding the lachrymal (1st infraorbital) and dermosphenotic, only three bones in this series. However, the elongate 'third' element shown in his figure is, in fact, two bones, the upper of which is the shorter.

Laterally, the second infraorbital canal overlaps the posterior margin of the lachrymal. There is some interspecific variability in the extent of this overlap. *Hemichromis fasciatus* has only the tubular part of the second infraorbital continued forward, but in *H. bimaculatus* the flange of bone underlying the canal also extends onto the lachrymal. In all other respects the infraorbital series in the two species are similar.

POSTTEMPORAL AND SUPRACLEITHRUM (Fig. 10B)

Van Couvering (1982:20 & 22; fig. 10) recognised two types of *supracleithrum* in the cichlids she studied. In the supposedly plesiomorphic etropline type (which includes the tilapiine species examined by Van Couvering) the posterior opening for the lateral-line tubule is situated near the dorsal tip of the bone. In the supposedly derived haplochromine type the opening lies much further down, generally at a level slightly above the midpoint of the bone's posterior margin. Using that classification, *Hemichromis* has a haplochromine type of supracleithrum. The validity of Van Couvering's postulated polarity ratings for this feature remain to be tested on a much larger assemblage of species.

There are no obviously outstanding features in the morphology of the *posttemporal* (Fig. 10B). However, this element is rarely used in cichlid systematics and hence is not often illustrated or described.

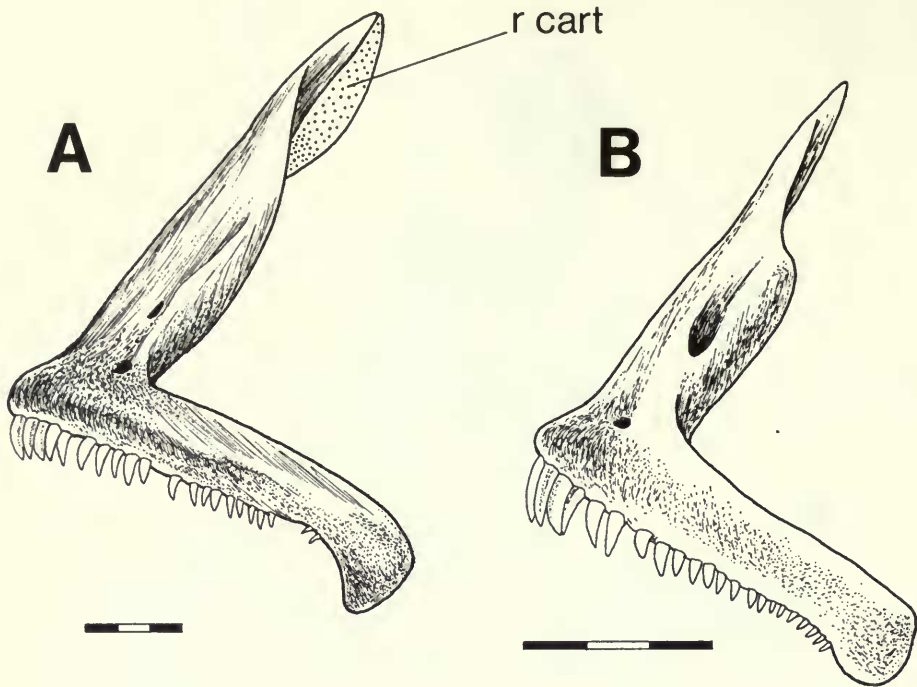


Fig. 11 A. *Hemichromis fasciatus*: premaxilla and rostral cartilage; left lateral view (1953.4.28:243-4).
 B. *H. bimaculatus*: premaxilla in left lateral view; rostral cartilage removed (unregistered specimen).

JAWS (Figs 6, 11, 12, 21)

The dentigerous arm of the *premaxilla* in *H. fasciatus* (Fig. 11A) is sharply and characteristically decurved posteriorly, with the result that its tip lies well below the level of the dentigerous area. The articular process extends distally along the lateral aspect of the ascending process almost to its tip; distally, the posterior margin of the articular process curves forward to become continuous with the anterior face of the ascending process. The rostral cartilage (Fig. 11A) is a relatively flat body, oval in outline, and with a maximum breadth only slightly exceeding those parts of the ascending process behind which it lies.

In *Hemichromis bimaculatus* (Fig. 11B) the posterior tip of the dentigerous arm is much less decurved, and the distal part of the articular process is more discrete than that in *H. fasciatus* (cf Figs 11A & B).

Both species have the length of the ascending process slightly less than the length of the dentigerous arm.

The other *Hemichromis* species show some variation in the degree to which the posterior tip of the premaxilla is decurved. In *H. frempongi*, *H. paynei* and *H. elongatus* the curvature equals that in *H. fasciatus*, but the condition in the remaining species is close to or identical with that in *H. bimaculatus*.

Maxilla (Fig. 12). Regan (1922) used the shape of the maxilla ('... maxillary narrow, curved') as one of two diagnostic features distinguishing *Hemichromis* from *Haplochromis*, the latter genus then containing the majority of fluviatile and lacustrine species in which the pharyngeal apophysis is of the *Haplochromis* type (see Greenwood, 1979). The maxilla in *Hemichromis* certainly does have a distinctive curvature (Fig. 12B) but in that feature it is approached, and equalled, by certain haplochromine species from Lake Victoria, although not by any of the generalized fluviatile species formerly identified as *Haplochromis* (see Greenwood, 1979). It was

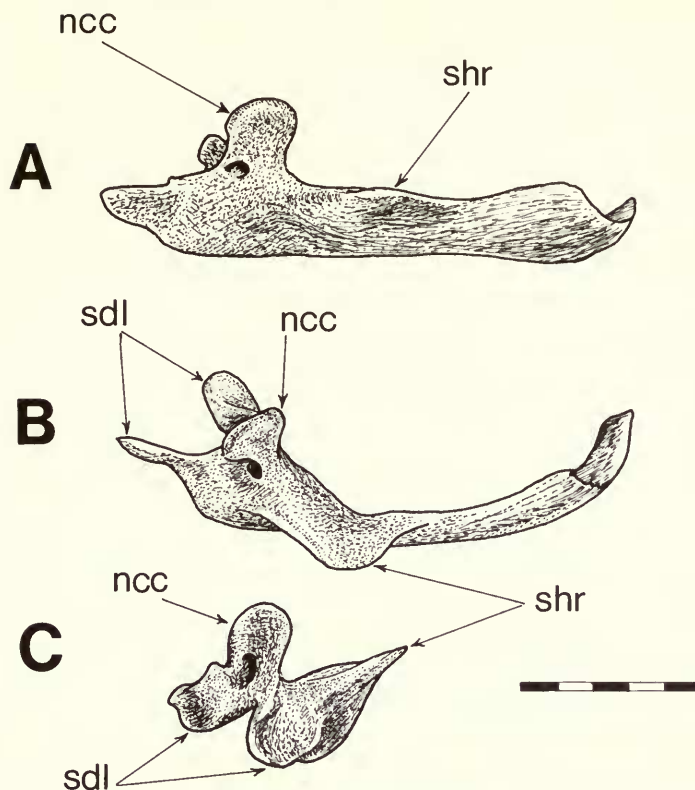


Fig. 12 *Hemichromis fasciatus*. Left maxilla in: A. Lateral, B. Dorsal, and C. Anterior views (1953.4.28:243-4).

these latter species with which Regan (1922) was presumably making his comparison since his paper was concerned with African and Syrian genera not restricted to the Great Lakes.

In dorsal view, the posterior part of the maxillary outline in *Hemichromis fasciatus* is a little more curved than it is in *Astatotilapia desfontainesi* (formerly a *Haplochromis*; Greenwood, 1979) and other generalized haplochromines. Anteriorly, however, the bone's mediad curvature is slightly less than in *A. desfontainesi* with the lateral arms of its premaxillary saddle lying in almost the same line as the anterior part of the shank (Fig. 12B).

When viewed laterally, the *Hemichromis* maxilla is relatively shallow, and the shank ridge is inclined outwards at a marked angle (Fig. 12A & C), both features distinguishing it from the maxilla in other African taxa.

The maxilla in *H. bimaculatus* has a more marked medial curvature than it does in *H. fasciatus*, is deeper, and its shank ridge inclines outwards at less of an angle. Also, in the former species the two arms of the premaxillary saddle are almost equal, whereas in *H. fasciatus* the lateral arm is noticeably longer.

Dentary (Fig. 6). In both *H. fasciatus* and *H. bimaculatus* the dentary is relatively short and moderately deep. It lacks a mental prominence in the symphyseal region with the result that the chin is gently rounded and slopes posteroventrally. The ascending coronoid arm is slender in *H. fasciatus* but is wider in *H. bimaculatus*.

Both species have four external openings to the mandibular laterosensory canal, an unusual feature in cichlids where, as far as I can determine, the usual number is five. There are, however, only four, and in some species three, openings in *Etroplus*. The phyletic significance of mandibular pore numbers is uncertain. Amongst lower perciforms there are four or five, and in the labroids (excluding cichlids) three or four.

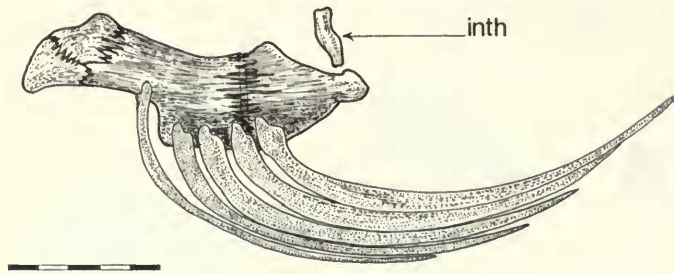


Fig. 13 *Hemichromis fasciatus*. Lower elements of left hyoid arch (excluding the basihyal), and branchiostegal rays; lateral view. (1976.11.12:135-137).

The posterior face of the vertical arm of the anguloarticular is expanded laterally, forming a distinct ledge onto which the *adductor mandibulae* 2 muscle inserts. The ledge in *H. bimaculatus* is relatively broader than that in *H. fasciatus*, and is distinctly concave (see comments in Stiassny, 1981a: 82-83, and Greenwood, 1983: 261).

An outstanding feature is the absence of a tunnel through the anguloarticular for the passage of the mandibulo-preopercular laterosensory canal in the ten species which could be thoroughly checked. Any connecting tubule between the laterosensory canals of the dentary and the preoperculum presumably must lie in the soft tissues of the region, but this could not be confirmed, with certainty, by dissection.

The absence of a laterosensory canal in the anguloarticular is a most unusual feature, one which has not been described in any other cichlids, and which with one exception (see p. 168) was not found in any of the numerous osteological preparations I examined.

HYOID ARCH AND UROHYAL (Figs 6, 13 & 10A)

Little has been published on the hyoid arch in cichlid fishes (Vandewalle, 1971; Goedel, 1974, Barel *et al*, 1976) and since I did not study these elements in taxa other than *Hemichromis*, few comparative statements can be made.

The hyoid arch (Fig. 13) seems to differ but slightly from that in *Astatotilapia elegans*, described in detail by Barel *et al* (1976), although in *Hemichromis* there is relatively less distance between the articulatory points for the first and second branchiostegal rays.

The morphology of the urohyal in cichlids has also been little studied (see Stiassny, 1981a:98). This bone in *Hemichromis fasciatus* (Fig. 10A) is somewhat elongate, with a prominent, anteriorly directed spine, and well-defined ventral wings enclosing a deep ventral wing fossa (terminology that of Barel *et al*, 1976). Dorsally, the base of the spine is continued backwards as a low ridge extending over about two-thirds of the bone's posterior length. The ridge runs the entire length of the dorsal ridge-groove but is displaced dextrally so that the right side of the groove is much smaller than the left, persisting merely as a ledge along the spine's posteriorly attenuated base. In those respects the urohyal of *Hemichromis fasciatus* differs quite markedly from that in *Astatotilapia elegans* (see Barel *et al* 1976:237, fig. 40).

DORSAL GILL-ARCH SKELETON (Figs 14B, 15 & 16)

The overall morphology and arrangement of these elements closely approach those of *Astatotilapia calliptera* and *A. elegans* (see Stiassny, 1981b, fig. 6 and Barel *et al*, 1976), a pattern which can be taken to represent the modal African cichlid condition.

As in *Astatotilapia*, pharyngobranchial 2 lies at right angles to the long axis of pharyngobranchial 3, and is directed transversely across its anterior border. Pharyngobranchial 3 differs slightly from that element in *Astatotilapia* because of its more nearly square outline. As in *Astatotilapia* it is intimately associated with upper pharyngeal tooth plate 4.

All four epibranchials, but particularly those of arches 1 and 2, are relatively more elongate than their counterparts in *Astatotilapia*, but are not as elongate as those in *Cichla* (see Stiassny, 1982: 431, fig. 2).

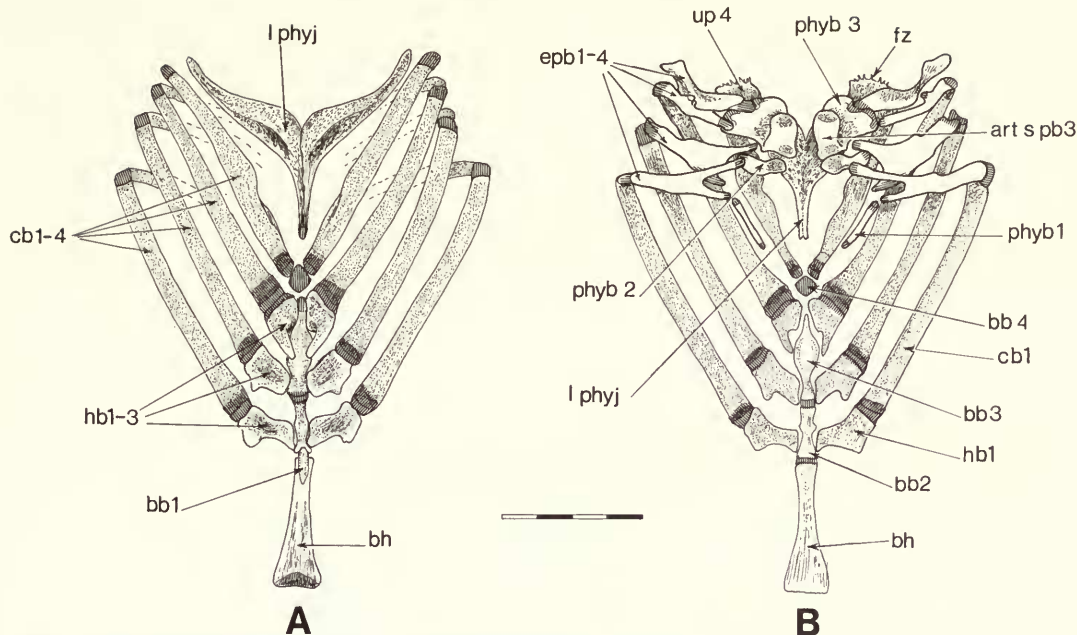


Fig. 14 *Hemichromis fasciatus*. Gill-arch skeleton in: A. Ventral, and B. Dorsal views (1976.11.12:135-7; alizarin-alcian blue transparency).

The angle formed between the two arms of epibranchial 1 is about 25° ; the posterior arm is almost twice the length of the anterior one and is directed caudad relative to the major axis of the bone. In the two latter characters, epibranchial 1 exhibits what seems to be the typically 'African' condition for the bone, but the angle between the arms is less than in other African species and thus approaches the condition usual in Neotropical taxa (Cichocki, 1976:84, fig. 1.16). My observations on the condition of epibranchial 1 in *Hemichromis fasciatus* differ somewhat from those of Cichocki who, unfortunately, gave no illustration of the bone in this species. According to Cichocki (1976:84), the two arms make an angle of 35° or more, and the posterior arm is directed strongly caudad.

The full significance of these various characters is difficult to assess because so little information is available from African taxa. Cichocki (1976:84) has, however, provided many data for the Neotropical species, and also discusses their possible phylogenetic significance.

As in *Astatotilapia*, and many other African taxa, but unlike *Cichla* and many Neotropical taxa (see Stiassny, 1981:295), there is no interarcual cartilage in *Hemichromis*.

Epibranchial 2 differs from that in *Astatotilapia*, and most other cichlids in which the feature has been checked, in having a very greatly reduced cartilaginous extension to its anterior border (Stiassny, 1981a & b, 1982; Barel *et al.*, 1976; Trewavas, 1973; personal observations). In *Hemichromis* only the protracted tip of the cartilage is visible as a projection below the anterior margin of epibranchial 1. The cartilage is reduced, and probably more so, in *Cichla* (see Stiassny, 1982: 431, fig. 2) and in *Orthochromis machadoi*, an African species (Greenwood, 1984: 210).

Epibranchial 4 articulates with pharyngobranchial 3, but has a strong ligamentous connection with the head of the 4th upper pharyngeal tooth plate as well (see Stiassny, 1981b:293, footnote, for use of the term 4th tooth plate). A prominent 'frayed zone' is associated with the posterior margin of the tooth-plate.

The quadrangular region (*sensu* Barel *et al.*, 1976) of epibranchial 4 has a more elongate outline and is less expansive in *Hemichromis* than in most African cichlids examined (see Figs 15 & 16) or those illustrated elsewhere (Barel *et al.*, 1976; Stiassny, 1981a & b, 1982). It would thus appear to

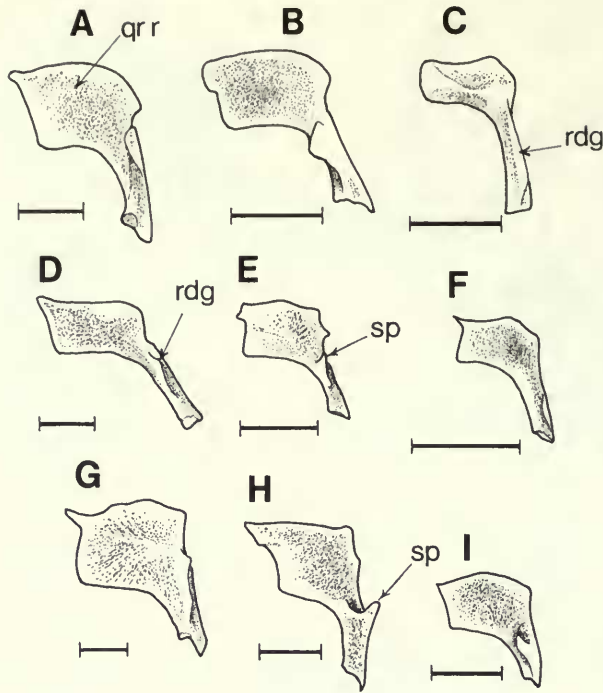


Fig. 15 Fourth epibranchial bone (right), in posterior view, of various cichlids to show outline of quadrangular area and variation in the development of the shank spine or ridge. A. *Astatotilapia macropsoides* (unreg. specimen). B. *Chromidotilapia kingsleyae* (1934.8.31:179-188). C. *Cichla ocellaris* (1973.3.26:1-6). D. *Hemichromis fasciatus* (1976.11.12:135-7). E. *Chromidotilapia finleyi* (1973.5.4:63-7). F. *Aequidens portalagrensis* (1972.10.17:3538-51). G. *Ptychochromis oligacanthus* (1882.2.25:173). H. *Oreochromis niloticus* (1960.9.30:158-72). I. *Trematocara unimaculatum* (1961.11.22:519-525).

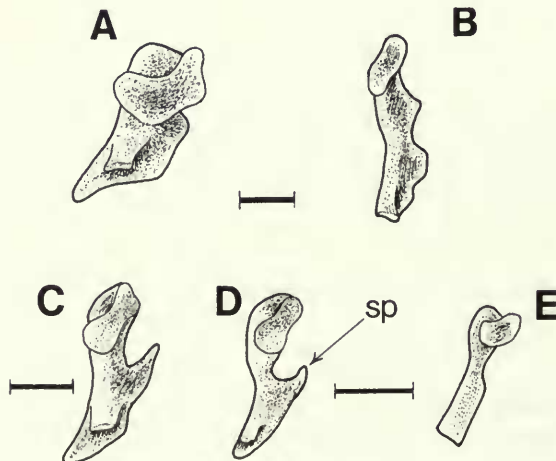


Fig. 16 Fourth epibranchial (right) in medial view to show variation in development of the shank spine or ridge in: A. *Ptychochromis oligacanthus*. B. *Hemichromis fasciatus*. C. *Astatotilapia macropsoides*. D. *Chromidotilapia kingsleyae*. E. *Cichla ocellaris*.

represent the plesiomorphic state for this character (personal observations and comments in Stiassny, 1981*b*). The shank spine on epibranchial 4 is little more than a low ridge, albeit a well demarcated one (Figs 15 & 16). In this respect it is intermediate between the condition seen in Neotropical taxa and that in the Madagascan etropline *Ptychochromis* where the ridge, although shorter is somewhat more elevated; the ridge in the Neotropical species is very low and long.

Judging from the condition of the shank spine (or ridge) in serranids, centropomids and non-cichlid labroids, a well demarcated spine is the derived condition. Amongst African cichlids, the type of ridge found in *Hemichromis* must therefore be considered plesiomorphic.

VENTRAL GILL-ARCH SKELETON (Fig. 14A)

Loiselle (1979) describes and illustrates the lower pharyngeal bones and dentition in all the *Hemichromis* species recognized by him. Apart from the lower pharyngeal bone, ventral gill-arch elements have been little used in cichlid systematics. That fact, combined with the very unsatisfactory condition of the gill arches in most skeletal preparations available to me, preclude any detailed comments on these bones in *Hemichromis*.

MICROBRANCHIOSPINES

According to Loiselle (1979:11), microbranchiospines are not present in any species of *Hemichromis*, a statement which is completely contradicted by my observations. These show that microbranchiospines are present on the outer aspect of gill arches 2 to 4 in *H. fasciatus*, *H. bimaculatus*, *H. letourneauxi*, *H. cerasogaster*, *H. guttatus*, *H. frempongi* and *H. paynei*; suitable material of the other species was not available.

In at least some individuals of *H. fasciatus*, microbranchiospines are present on both faces of certain arches. An alizarin preparation, ca 80 mm standard length (BMNH 1976.11.12:135–7), has these structures on the outer face of arch 2, on both faces of arch 3 (but probably restricted to the lower part of the inner face), and on both faces of arch 4 (again probably with a restricted distribution, in this instance to the upper regions).

A double-sided distribution was not found in other *H. fasciatus* specimens (both stained and unstained, in the size range 60–120 mm SL), nor was it found in any other species of the genus. Interestingly, Stiassny (1981*b*:304) records microbranchiospines on both sides of arches 1–4 in *Cichla* and *Etoplus*. To the best of my knowledge there are no records of other cichlid species showing a similar distribution pattern.

CAUDAL SKELETON (Fig. 17)

Those specimens of *H. fasciatus* which I examined differ in no appreciable way from that illustrated by Vandewalle (1973:fig. 1). That figure does not, however, indicate the cartilages associated with the fin skeleton, some of which are shown in Fig. 17 below. Although not represented in that figure, cartilage is also present along the posterior margin of the epurals, hypurals, parhypural and the haemal spine on the second preural vertebra. Because the cartilage has stained irregularly in the specimens I examined it is impossible to tell whether, as in *Cichla*, it is in the form of two bands continuous with, respectively, the dorsal and ventral accessory cartilage masses (see Fig. 17). Certainly there is no trace of a cartilage plate between and connecting hypurals 2 and 3, a feature which Stiassny (1982:450) considers an apomorphy of *Cichla*.

In two alizarin-alcian blue stained specimens of *H. bimaculatus* the caudal skeleton differs from that in *H. fasciatus* in having no hypurapophysis on the parhypural, and in having a less expansive neural arch and spine on the second preural centrum.

Both *H. fasciatus* and *H. bimaculatus* have I+7, 7+I principal caudal rays, together with a number of much shorter rays preceding them.

No fused hypurals were found in the specimens of *H. fasciatus* examined, although hypurals 1 and 2, and 3 and 4 are very closely apposed. In one *H. bimaculatus* none of the hypurals is closely apposed, but in other specimens hypurals 3 and 4 are closely applied to one another along their entire lengths.

From what is known about the caudal fin skeleton in cichlid fishes it does not seem likely that it will prove to be of use in determining intrafamilial relationship (see also Vandewalle, 1973).

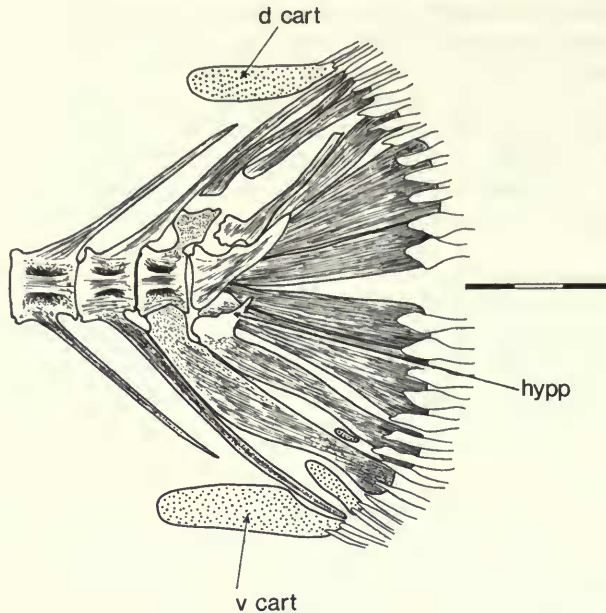


Fig. 17 *Hemichromis fasciatus*. Caudal fin skeleton; only the larger cartilages are illustrated. (1976.11.12:135-7).

PECTORAL GIRDLE (Fig. 18)

The pectoral girdle apparently provides few characters of value for establishing phylogenetic relationships amongst the cichlids (see Cichocki, 1976; Stiassny, 1982).

Both these authors note the presence in the Neotropical genera *Cichla* and *Crenicichla* of a prominent, anterodorsally directed spine on the head of the second postcleithrum, and Stiassny (1982:448) records a small process, similarly directed, on the head of that element in three other Neotropical genera, *Petenia*, *Acaronia* and, in some species, *Cichlasoma*. In *Cichla* and *Crenicichla* the process is associated with a sheet of muscle extending from the first pleural rib, but in the other species the process does not serve as a site for muscle attachment (Stiassny, 1982:448).

A small and short, but obvious process is present on the second postcleithrum in *Hemichromis* (Fig. 18B); it is less well differentiated than the process in *Petenia*, and, as in that species, it does not seem to be associated with a muscle sheet from the first rib. The presence of this short process gives the head of the second postcleithrum a more rectangular and broader outline than that present in other African and in Neotropical species.

Stiassny (1982:448) discusses the phyletic significance of the postcleithral process, especially in relation to its presence in *Cichla*, *Crenicichla* and the serranid genus *Serranus*. She favours homoplasy as an explanation of these interfamilial occurrences. The reduced (or poorly developed) spine in *Hemichromis* and in certain Neotropical taxa is probably open to the same interpretation.

VERTEBRAL COLUMN

An apophysis for the origin of the *retractor arcuum branchialis* muscles, Trewavas' (1982:9) spondylophysal apophysis, is developed on the third abdominal vertebra in *H. fasciatus* and *H. bimaculatus*; its presence could not be checked in the radiographs of the other species.

Epipleural ribs are present on all but the last 3 or 4 pairs of pleural ribs in both species, and epicentral ribs occur on the first two centra (which do not carry pleural ribs).

None of these features could be determined with certainty (or even at all) from the radiographs

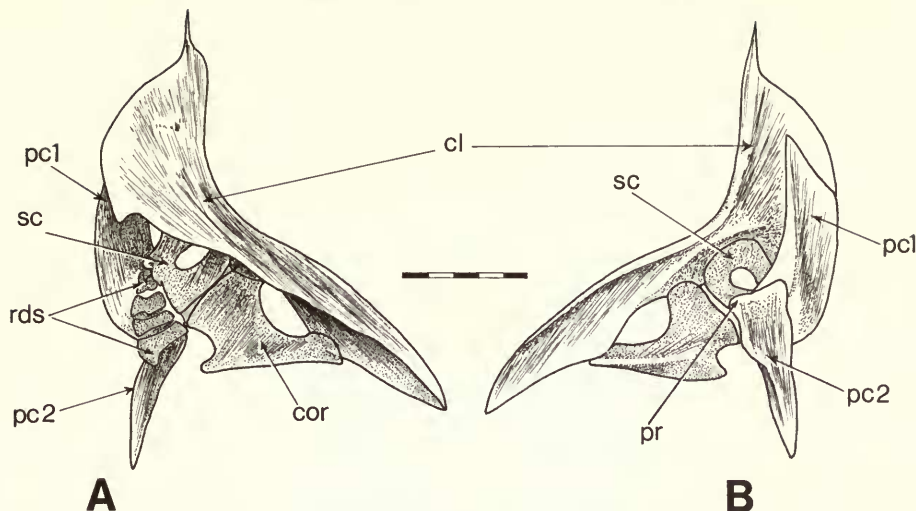


Fig. 18 *Hemichromis fasciatus*. Pectoral girdle in: A. Lateral view, B. Medial view (1976.11.12:135–7).

of the other *Hemichromis* species. *Vertebral counts* were made, and are listed below. It would seem from those figures that two intrageneric groups can be recognised, one with a higher total count (*ie* 26–28, mode 27) than the other (25, less frequently 26). The higher count is attributable to an increase in the number of abdominal centra.

In the list below, frequencies are indicated by *f*, and modes are in bold type. The fused PU_1 and U_1 centra are excluded from all counts.

Group I:

H. fasciatus: 27 or **28**, comprising **15** abdominal + 12 (*f*5) or **13** (*f*7) caudal centra

H. elongatus: 26 or **27**, comprising 14 (*f*1) or **15** (*f*11) + **12** (*f*12)

H. fremongi: **27** (*f*13) or 28 (*f*2), comprising 14 (*f*1) or **15** (*f*14) + **12** (*f*12) or 13 (*f*3)

Group II:

H. bimaculatus: **25** (*f*7) or 26 (*f*1), comprising **13** (*f*6) or 14 (*f*2) + 11 (*f*1) or **12** (*f*7)

H. cristatus: 25 comprising 12 + 13 (Holotype: 1969.3.26:76)

H. paynei: **25** (*f*17), comprising **13** (*f*17) + **12** (*f*17)

H. guttatus: **25** (*f*2), comprising **13** (*f*2) + **12** (*f*2)

H. stellifer: **25** (*f*3) comprising **13** (*f*2) or 14 (*f*1) + 11 (*f*) or **12** (*f*2) (Paratypes AMNH 16864)

H. cerasogaster: **25** (*f*4) comprising **13** (*f*4) + **12** (*f*4)

H. letourneauxi: **25** (*f*15) or 26 (*f*5), comprising 12 (*f*2) or **13** (*f*18) + **12** (*f*14), 13 (*f*5) or 14 (*f*1)

H. lifalili: **25** (*f*5) comprising **13** (*f*5) + **12** (*f*5)

Myology

JAW MUSCLES (Figs 19–21)

As Vandewalle (1971:271; fig. 6) noted in his description of *H. fasciatus*, these muscles are well-developed. *Adductores mandibulae* 1 and 2 are bulky, with *Adductor* 2, at its midpoint, about two and three quarters times deeper than *Adductor* 1 (Fig. 19). *Adductor* 3 is also a large muscle, the lower part of which exchanges fibres with *Adductor* 2; it inserts on the coronomeckelian ossification.

The A_w division of the adductor complex covers about two-fifths of the inner aspect of the lower jaw (Fig. 21). As compared with the condition of this muscle in those cichlids in which it has been described (Anker, 1978; Stiassny, 1981*a* & *b*, 1982), the central aponeurosis is reduced and, consequently, the muscle is more musculose; its fibres, particularly those on the lower half of the muscle, are arranged almost horizontally. Posteriorly A_w has a tendinous attachment to the medial face of the quadrato (Fig. 21). At that point the tendon is narrow, and remains narrow as it passes across the quadrato-mandibular joint.

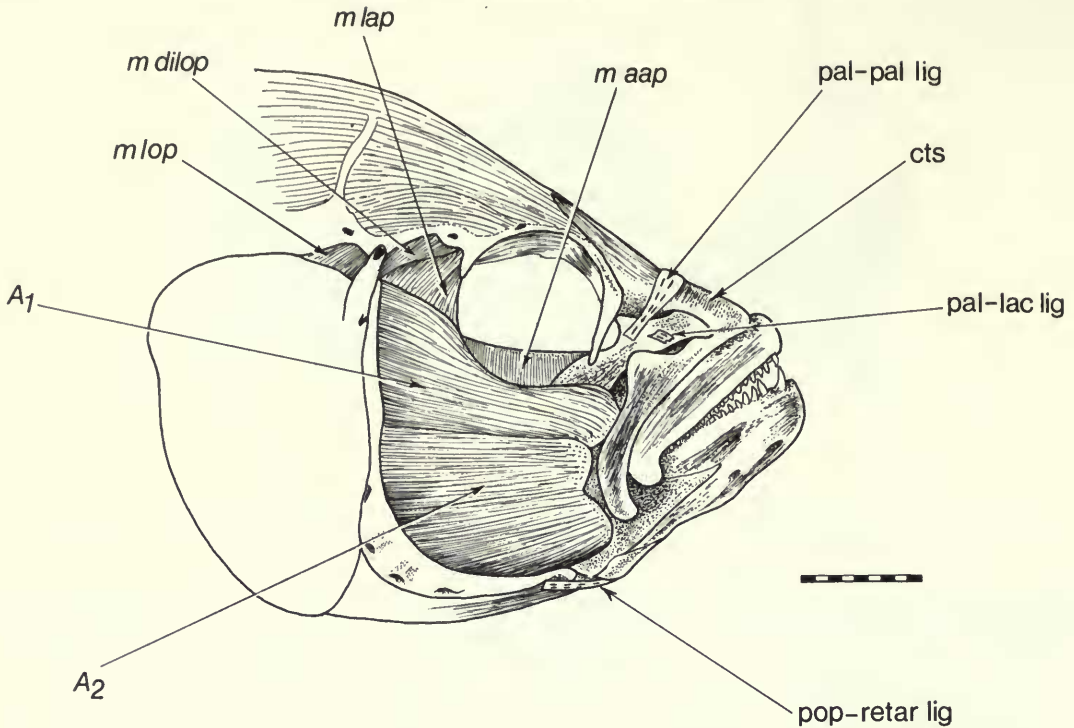


Fig. 19 *Hemichromis fasciatus*. Superficial muscles of the jaw and suspensorium, and superficial jaw ligaments. Only the proximal end of the palatolachrymal ligament remains after removal of the lachrymal bone (1953.4.28:423-4; 115 mm SL).

Unlike the tendon A_{1b} described in other cichlids, the A_{1b} tendon in *Hemichromis fasciatus* first merges completely (and not just partially) with the tendon of A_w before, as a discrete entity again, it inserts on the nipple process of the anguloarticular (Fig. 21).

The origins and insertions of the adductor complex follow the usual cichlid pattern (see Anker, 1978; Stiassny, 1981a & b, 1982). The stout tendon of *Adductor 1* has a long area of insertion ventrally on the anteromedial face of the maxilla, extending between the neurocranial condyle of that bone and a line drawn through the anterior margin of its shank ridge.

An *intermandibularis* muscle is present, and has no outstanding features.

The *levator arcus palatini* (Figs 18 & 19) is a bulky muscle, rhomboidal in outline. It originates on the sphenotic and inserts onto the hyomandibula and upper part of the metapterygoid. Its insertion is confined to the lateral, that is outer, aspects of these bones since no calyx is developed (see p. 145).

The *adductor arcus palatini* (Figs 19 & 20) is a thick, well-developed muscle, from which a small anterior portion extends forward onto the palatine, filling the recess in the posterior part of that bone (see p. 144) and the recess in the dorsal part of the ectopterygoid. No such extension of the muscle was noted or figured by Vandewalle (1971:271; fig. 5), but its presence in all specimens of *H. fasciatus* (and those examined by Cichocki [1976]) suggests that it must have been overlooked by that author.

A palatinad extension of the *adductor arcus palatini* is a characteristic of all the African cichlids I have examined and those studied by Cichocki (1976), although it is absent in *Heterochromis* (M. K. Oliver, pers. comm.). No extension was found in the many Neotropical cichlids examined by Cichocki, and it is also wanting in the etropline species, including those from Madagascar, which he examined (Cichocki, 1976: 201).

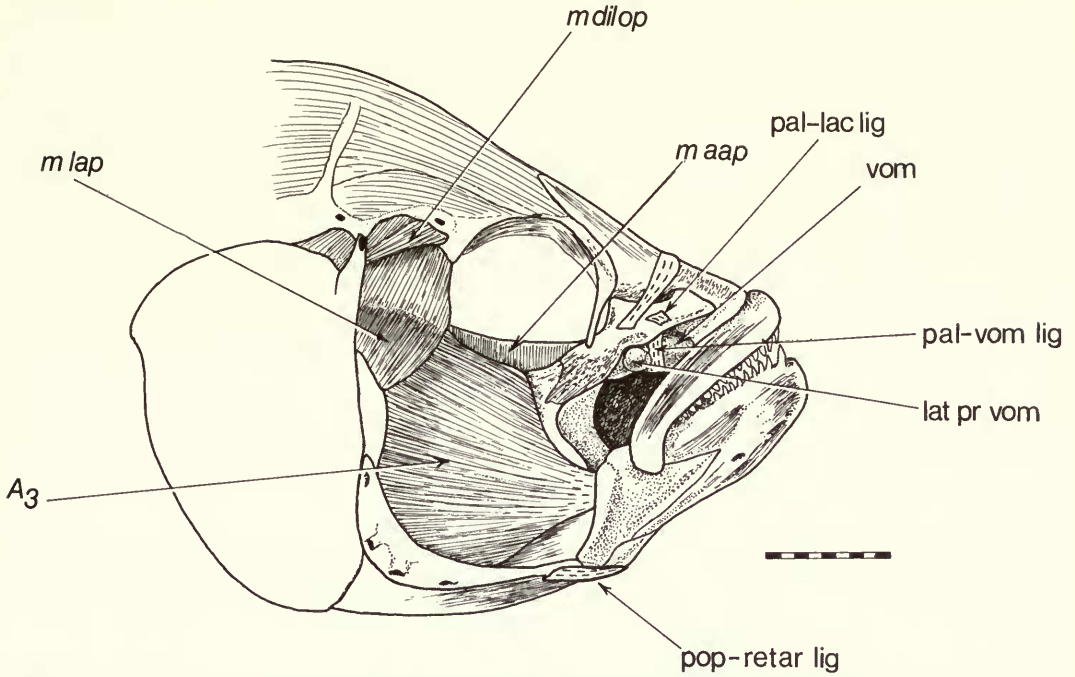


Fig. 20 *Hemichromis fasciatus*. Deeper jaw and suspensorium muscles. The maxilla has been removed to show, in part, the palatovomerine ligaments and also the lateral process of the vomer articulating with the palatine.

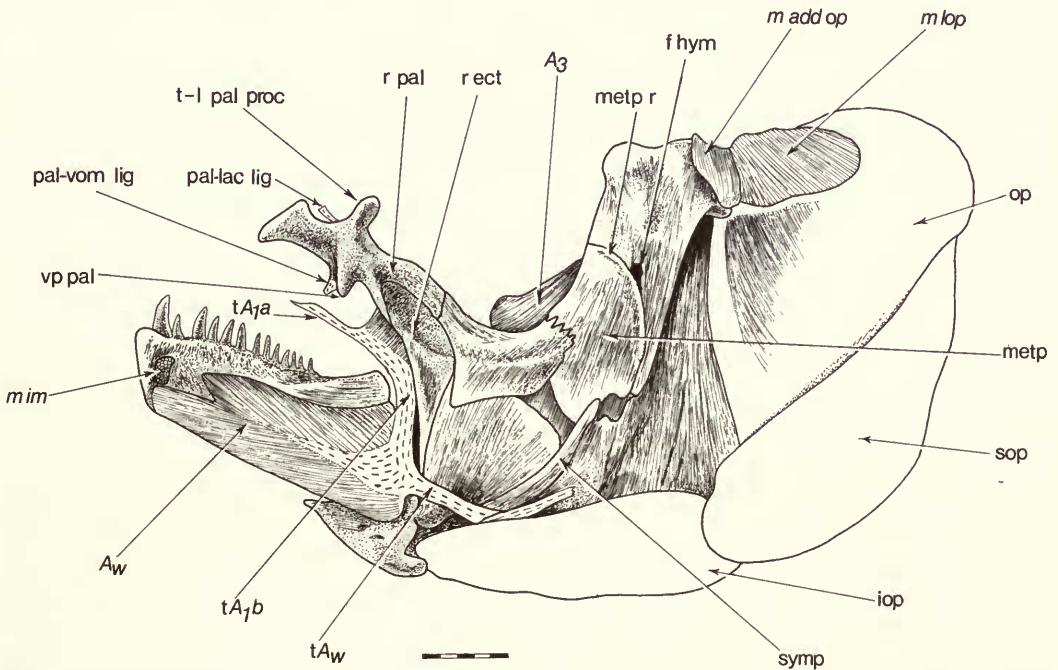


Fig. 21 *Hemichromis fasciatus*. Medial view of right suspensorium and dentary to show the A_w muscle and its tendons, and the tendon system associated with *m. adductor mandibulae* 1. The articular processes of the palatine, and the recessed medial faces of the palatine and ectopterygoid (for the insertion of the extended *m. adductor arcus palatini*) are also visible.

LIGAMENTS ASSOCIATED WITH JAWS AND PALATOPTERYGOID ARCH IN *H. fasciatus* (Figs 19–22)

A broad swathe of very dense connective tissue extends across the ascending processes of the premaxillae, connecting the maxilla and palatine of each side, and those of opposite sides, with one another. Its points of origin are along the anterior margin of each maxilla (from the anterodorsal tip to the level of the facet for articulation with the palatine), and from the anterodorsal margin of the palatine, including the triangular prominence (see p. 143). Dorsally, this sheet is continuous with the lower margin of the palato-palatine ligament which, however, is readily distinguishable by its more densely compacted tissue, and hence its appearance.

The *palato-palatine* ligament itself originates on each palatine from a marked prominence below the ethmoid articulatory process of the bone. It broadens as it passes across the premaxillary ascending processes, where it appears to become continuous with the connective tissue sheet described above.

Anterior to, and a little below the level of the boss to which the palato-palatine ligament is attached, there is a shallow, elongate groove on the lateral face of the palatine. A broad-based ligament, the *palatolachrymal*, originates from this groove, and inserts on the lachrymal (1st infraorbital bone). Vandewalle (1971; fig. 5) illustrates a ligament in this position (labelled li3) which he identifies as the palato-maxillary ligament. There are, however, no palato-maxillary ligaments in this position in *H. fasciatus*; Vandewalle's li3 is, in fact, the proximal part of the palato-lachrymal ligament, its distal portion having been detached with the lachrymal bone during dissection (see Figs 19–21).

The absence of well-defined *palatomaxillary* ligaments in *Hemichromis* is a most noteworthy feature. In all other African cichlids examined a clearly defined ligamentous band passes over the palato-maxillary articulation, attaching the palatine head to the underlying lateral face of the maxilla (ie Cichocki's [1976:81] *anterodorsal palatomaxillary* ligament); in *Hemichromis* there is only a weak connective tissue linkage between the bones at this point, or at most a few clearly ligamentous strands of tissue. In the other African cichlids I examined there is a second and strong ligament which, originating from a discrete process below the spur for the palato-palatine ligament, inserts on the head of the maxilla immediately behind the anterodorsal palatomaxillary ligament. This ligament Cichocki (1976: 80–81) calls the *anteroventral palatomaxillary* ligament. It too is absent in *Hemichromis* (specimens of all species except *H. cristatus* were dissected).

Cichocki (1976:81) comments on the absence of an anteroventral palatomaxillary ligament in the Neotropical cichlids, and its presence in all the African species he examined and in others studied by Liem & Osse (1975), ie *Astatotilapia burtoni*, *Oreochromis niloticus*, *Tropheus moori* and *Eretmodus cyanostictus*. I can confirm its presence in all the African species I dissected (see p. 133), except, of course, *Hemichromis*. Another African species, *Pterochromis congicus* may also lack this ligament, but the material dissected was poorly preserved so its apparent absence in that species must be treated as unconfirmed.

An anteroventral palatomaxillary ligament is definitely present in the Madagascan and Asian etropline cichlids examined, viz: *Etroplus maculatus*, *Paretroplus dami*, *Paratilapia polleni* and *Ptychochromis oligacanthus* (see Cichocki, 1976; also pers. observations).

In all the eight *Hemichromis* species dissected (see p. 133) there are no vertically aligned *ethmopalatine ligaments* (Stiassny's [1981a] palatine lateral ethmoid ligament). This ligament, or ligaments since there may be two or even three contiguous divisions, is present in the majority of African taxa I examined, but it is absent in at least three species from Lake Tanganyika, *Bathybates*, *Hemibates* and *Trematocara* (see Stiassny, 1981:97; figs 13, 14 & 20). Fewer data are available on these ligaments in Neotropical species, but personal observations suggest that one or more is generally present.

It could be argued that the absence of lateral ligamentous connections between the ethmoid and palatine in *Hemichromis* is correlated with the unusual way in which the bony palato-ethmoidal joint has been effected in that genus (see p. 138). That argument cannot, however, be used to explain their absence in *Bathybates*, *Hemibates* and *Trematocara*. These species have the modal, and plesiomorphic, anterior palato-ethmoidal articulation found in other African cichlids, in many Neotropical taxa, and amongst lower percoids as well; see discussion on p. 166 below.

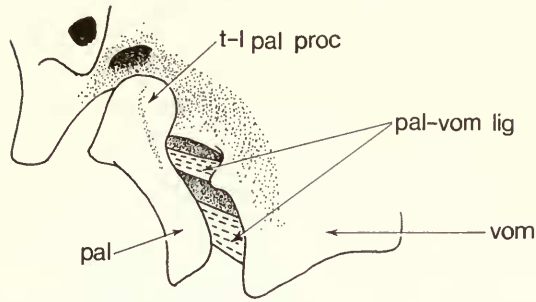


Fig. 22 *Hemichromis letourneauxi*. Semi-schematic sketch to show the typical *Hemichromis* type of palatovomerine ligament system; viewed from above and anterolaterally. The palatine bone has been dislocated from its articulation with the lateral ethmoid and moved a little outwards and downwards (1907.12.2:2969–84).

All the African and Neotropical cichlids I examined do have a posterior ethmo-palatine ligament, namely one between the posterior (*ie* intraorbital) face of the lateral ethmoid and the posterior wing of the palatine. In *Hemichromis* this ligament can be absent in one species, is thin and weakly developed in others, but is stout and well-developed in the majority. Vandewalle (1971:271, fig. 5) illustrates a posterior ligament in *Hemichromis fasciatus* and comments on its more posterior position in that species relative to *Tilapia guineensis*. However, Vandewalle appears to have confused the anterior palato-lateral ethmoid ligament in *T. guineensis* with the posterior and intraorbital ligament in *H. fasciatus*. The latter ligament is also present in *T. guineensis*, and occupies a position comparable with that in *H. fasciatus*.

At present little is known about the nature and occurrence pattern of palato-ethmoidal ligaments in percoids and especially in cichlids. Based on out-group comparisons with other percoids (eg Serranidae and Centropomidae) it seems that the presence of anterior palato-ethmoidal ligaments is a derived condition, but that a posterior (*ie* intraorbital) ligament is a primitive feature. Another 'primitive' ligament is that between the palatine and the mesethmoid; such a ligament is present in some cichlids (see Stiassny, 1981a:76) but is wanting in the majority, including *Hemichromis*.

Judging from the presence/absence pattern of lateral palato-ethmoid ligaments in cichlids, their absence might well be considered as a secondary loss (*ie* a derived condition), possibly one associated with the functional-structural characteristics of the bony palato-ethmoidal articulation. Until that possibility has been explored, both in cichlids and out-group taxa, little that is worthwhile can be said about their value as indicators of phyletic relationship.

There is a double *palatovomerine ligament* system in *Hemichromis* (Fig. 22). Ventrally, a strong ligament runs from the medial aspect of the palatine to insert on the ventrolateral face of the vomerine fossa, immediately in front of the lateral vomerine process on which the palatine articulates and is supported (see p. 138). Dorsally, a broad but less robust ligament connects the base of the thumb-like process on the palatine with the vomerine fossa; it inserts slightly above the ventral ligament.

DORSAL GILL-ARCH MUSCULATURE (Figs 23–25)

These muscles conform to what is apparently the typical cichlid pattern (see Anker, 1978; Stiassny, 1981a & b, 1982; Liem & Greenwood, 1981; Kaufman & Liem, 1982).

The *transversus dorsalis anterior* muscle, as in all cichlids, is tripartite, with the *musculus transversus pharyngobranchialis* 2 division marginally the smallest element, and the *m. cranio-pharyngobranchialis* 2 clearly the largest.

The *mm levatores externi* 1–3 are of approximately equal size. The fourth muscle is distinctly enlarged; the greater part inserts, through a short tendon, onto the horn of the lower pharyngeal bone (the fifth ceratobranchial). A small, lateral slip of this muscle inserts, tendinously, on the fourth epibranchial.

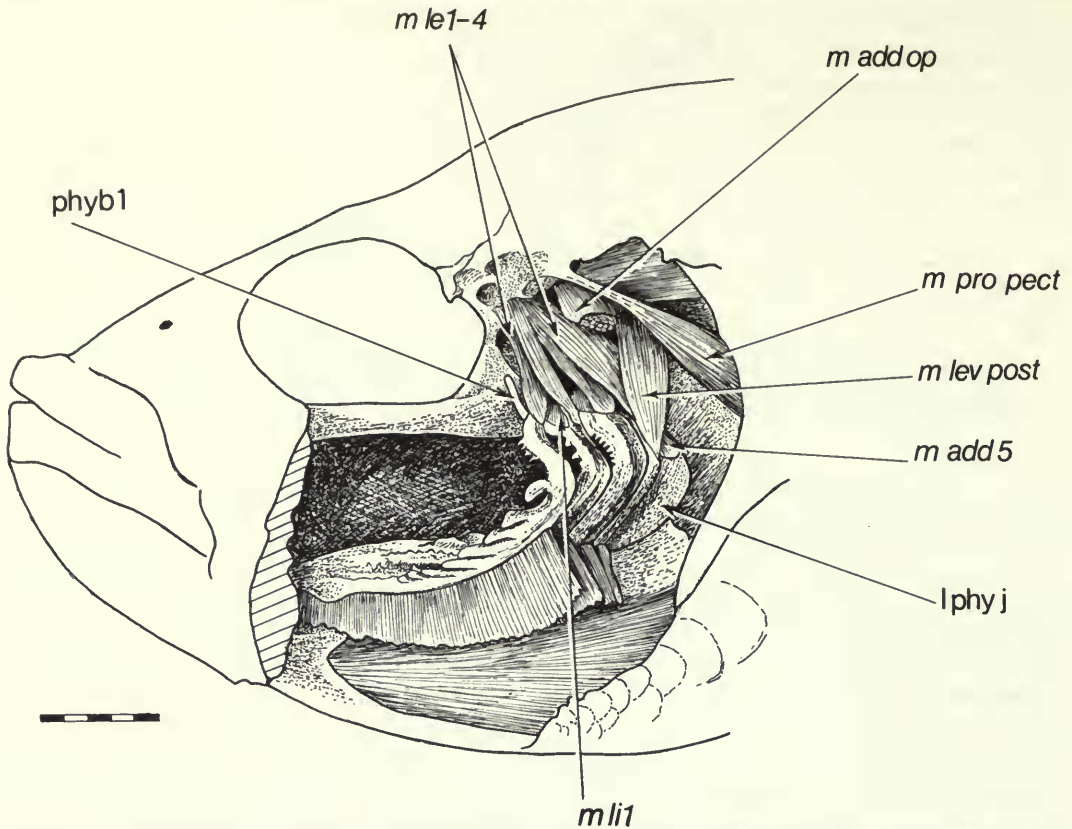


Fig. 23 *Hemichromis fasciatus*. Dissected head to show the superficial and lateral gill-arch musculature. Gill filaments have been removed from the upper parts of the gill-arches.

The two *mm levatores interni* are each of approximately the same bulk, with the second being very slightly the larger of the pair.

The *m. levator posterior* is well-developed, with a cross-sectional area about one third that of the *m. levator externus 4*. It inserts both on the fourth epibranchial, laterally, and on the horn of the lower pharyngeal bone medially. The greater part of its insertion, however, is on the epibranchial. Only a small slip is continuous with the underlying lateral division of the *m. obliquus dorsalis posterior* and thus comes to insert on the lower pharyngeal horn (see Aerts, 1984, whose terminology is followed here).

Based on the condition seen in certain other African cichlids I examined (eg *Aulonocranus dewindtii*) where there is greater continuity between the *m. levator posterior* and the lateral division of the *m. obliquus dorsalis posterior*, the situation in *Hemichromis fasciatus* must be considered plesiomorphic.

Hemichromis is not unique in this respect since it is paralleled in *Astatotilapia elegans* (see Anker, 1978), *Cichla ocellaris* (Stiassny, 1982; fig. 6; pers. obs.), and *Aequidens vittatus* (pers. obs.).

From the various published figures of the dorsal gill-arch musculature in cichlids, it would seem that the lateral division of the *m. obliquus dorsalis posterior* has either been overlooked or else treated as part of the fifth adductor muscle (which connects the fourth epibranchial with the horn of the lower pharyngeal bone). The role of the oblique posterior muscle in the evolution of cichlid pharyngeal jaw musculature was clearly demonstrated by Aerts (1982). A detailed study of increasing association between the oblique posterior and the posterior levator muscles in cichlids has yet to be made; it is this change which presumably underlies Kaufman & Liem's (1982) character 'Predisposition for insertion of levator posterior muscle on lower pharyngeal

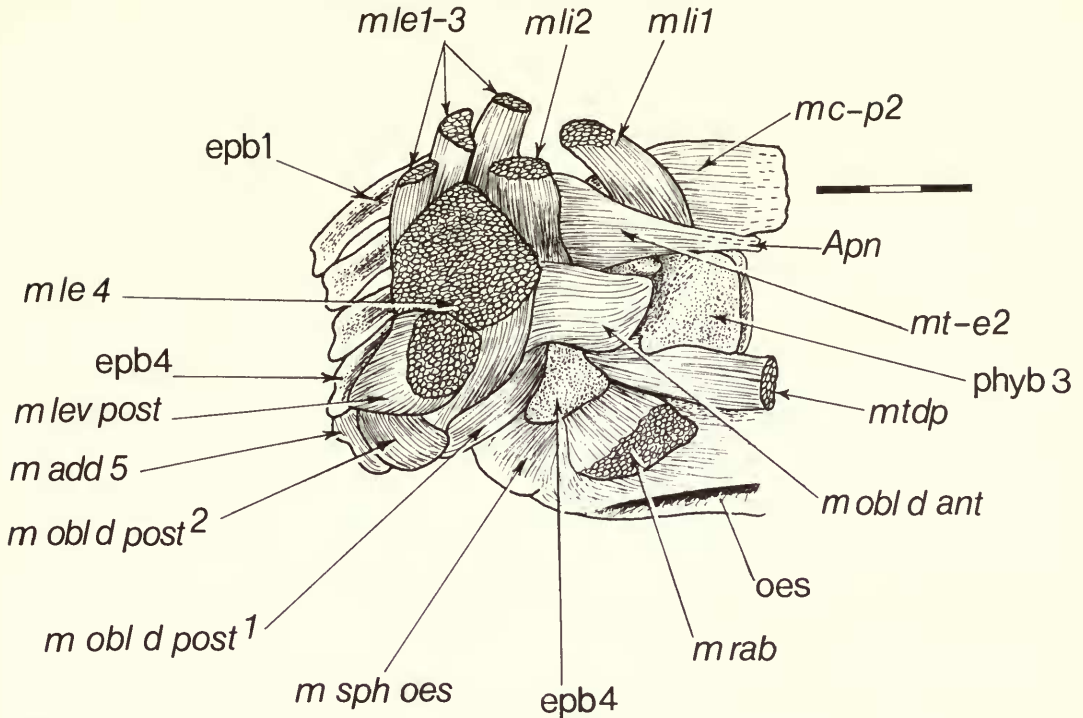


Fig. 24 *Hemichromis fasciatus*. Dorsal gill-arch musculature, in dorsal view. The *m. transversus pharyngobranchialis 2* is not visible since, in this view, it lies below the *m. cranio-pharyngobranchialis 2* muscle (1976.11.12:138-41).

jaw' which they cite as a synapomorphy for the cichlids, embiotocids and labrids; it is clearly a feature already manifest in several cichlids.

In *Hemichromis fasciatus* the medial division of the *m. obliquus dorsalis posterior* is a moderately substantial muscle, but is noticeably less voluminous than the anterior division of the *obliquus* complex.

On Stiassny's reckoning (1982:436; figs 7 & 8), the origins of the *mm levatores externi* and *interni* of *Hemichromis* are displaced caudally, and according to her a well-developed hyomandibulad shell is lacking in this taxon. In both these features Stiassny considers *Hemichromis* to be comparable with *Cichla*, certain other Neotropical taxa, and the Madagascan etropline *Paratilapia*. She also considers the features to be plesiomorphic ones.

The peculiarly developed and unique hyomandibulad shell, or rather hyomandibulad pit was discussed on p. 142. No comparable structure is present in *Paratilapia*, *Cichla* or the other Neotropical taxa listed by Stiassny, namely *Petenia*, *Chaetobranchius* and *Crenicichla*.

When viewed laterally the apparent origin of the *levatores externi* and *interni* muscles in *Hemichromis* begins at a line drawn vertically through the middle of the anterior facet of the hyomandibular head, and continues backward to a line drawn through the posterior hyomandibular facet. In other words, the origins of these muscles occupy an area comparable with that illustrated by Stiassny (1982: fig. 8) for *Astatotilapia*, which species she considers to have an 'anterior' area of origin for these muscles.

In actual terms rather than apparent ones, the *mm levatores externi* 1-4 in *Hemichromis fasciatus* originate mainly from the roof and sides of the hyomandibulad pit; the mediocaudal part of the fourth muscle, however, originates from the anterior boundary wall of the deep awning (see p. 142). The *mm levatores interni* 1 and 2 also originate from the hyomandibulad pit, which occupies an area almost identical with the triangular area of origin for the levator muscles in *Astatotilapia* illustrated by Stiassny (1982: fig. 8).

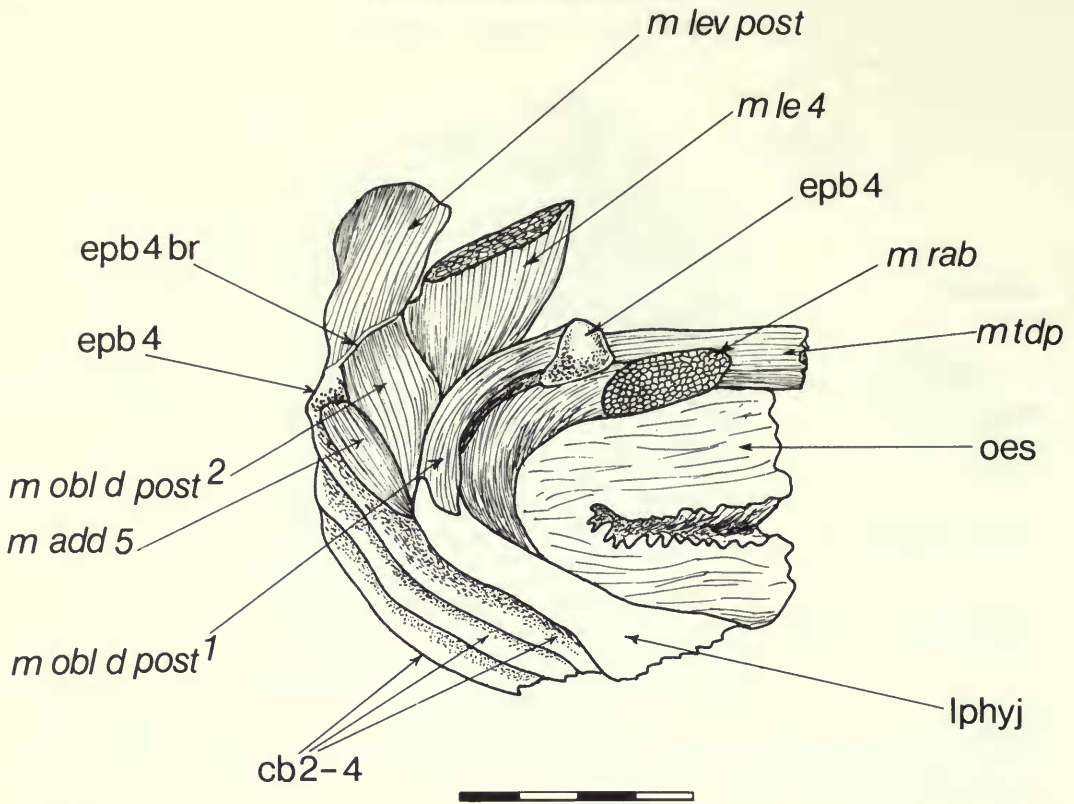


Fig. 25 *Hemichromis fasciatus*. Dorsal gill-arch muscles viewed from behind and a little ventrally. The *m. levator posterior* has been reflected laterally and somewhat anteriorly.

Thus, there would seem to be no grounds for considering the situation in *Hemichromis*, apart from the pit-like hyomandibulad shell, as being significantly different from that in *Astatotilapia*, nor is it like the presumed plesiomorph condition in *Cichla* and the other Neotropical taxa mentioned by Stiassny.

LATERAL AND VENTRAL GILL-ARCH MUSCLES

These muscles in *Hemichromis* were not studied in detail except to compare certain elements with those in *Cichla*, which Stiassny (1982: 437–442) described and commented upon, and others which were noted by Vandewalle (1971:271, fig. 5) in his account of *Hemichromis fasciatus*.

Stiassny (1982: 438) noted that in *Cichla ocellaris* certain elements of the 'muscular sling' associated with the lower pharyngeal jaw departed from the assumed modal cichlid condition seen in *Astatotilapia*. *Hemichromis*, in contrast, departs but slightly in these features from the *Astatotilapia* condition (Anker, 1978; Stiassny, 1982). For example, the B branch of the *m. pharyngocleithralis externus* in *Hemichromis* is much narrower below its division into the branches attaching to the lower pharyngeal bone and the fourth ceratobranchial respectively, and its muscose part is relatively much shorter than in *Cichla ocellaris*.

The *pharyngohyoideus* in *Hemichromis*, both in its insertion on the lower pharyngeal bone, and in its relationships with the tendons of *pharyngocleithralis externus* B, is like that muscle in *Astatotilapia*. Anteriorly it inserts along the dorsal surface of the urohyal, and terminates by inserting on the well-developed urohyal spine.

Vandewalle (1971:271; fig. 5) notes, apparently as a unique condition among the two African and three Neotropical cichlids he studied, that the *m. obliquus ventralis* 3 and the *m. rectus ventralis* insert on the third hypobranchial via '... un tendon en fer à cheval' (Anker's [1978]

semicircular ligament). Vandewalle's figure is somewhat misleading since it shows both muscles apparently inserting entirely on the ligament. That is so for the *rectus ventralis*, but the greater part of the *obliquus ventralis* 3 inserts directly onto the hypobranchial, to which bone the semicircular ligament is also attached. Indeed, it is only the medial margin of *obliquus ventralis* 3 which is associated with the ligament.

Involvement of these two muscles with a semicircular ligament is by no means unique to *Hemichromis*. Such an association is present, among African taxa, in *Serranochromis* (*Sargochromis*) *mellandi*, *Tilapia sparrmani*, *Astatotilapia burtoni*, *A. elegans*, *Aulonocranus dewindti*, *Rhamphochromis longiceps*, *Trematocara unimaculatum*, *Hemibates stenosoma*, *Thoracochromis buysi* and *Chromidotilapia guentheri* (personal observations; also Anker, 1978 for *Astatotilapia elegans*). The tilapiine species examined by Goedel (1974), *Tilapia tholloni*, *Oreochromis niloticus* and *Sarotherodon melanotheron*, show a similar arrangement.

Only one Madagascan species, *Paratilapia polleni*, could be dissected; it too shows the same arrangement as that in the species listed above. So too do two of the Neotropical species I examined, *Acarichthys heckeli* and *Chaetobranchius flavescens*. In two other Neotropical taxa, *Cichla ocellaris* and *Crenicichla saxatilis*, however, the insertions of *obliquus ventralis* 3 and *rectus ventralis* 4 are quite different, and resemble the condition found in the serranid *Serranus cabrilla*.

In *Cichla* there is no semicircular ligament; *obliquus ventralis* 3 is an elongate as opposed to a short muscle, and it inserts directly onto hypobranchial 3. *Rectus ventralis* 4 is also elongate, runs parallel and medial to *obliquus ventralis* 3, and also inserts on hypobranchial 3, but by a long and discrete tendon which passes through part of *obliquus ventralis* 3 before it attaches, independently, onto the hypobranchial.

The arrangement of the muscles in *Crenicichla* is essentially similar, but the *rectus ventralis* 4 is shorter.

Intrafamilial variability in the arrangement of these muscles also occurs, but is less extreme than that existing between *Cichla* or *Crenicichla* and the other species noted above. For example, in *Bathybates vittatus*, although much of the *obliquus ventralis* 3 inserts directly on the hypobranchial, and part also attaches to the ligament, there is a substantial, medially directed division which joins a similar division from its antimeres in a median aponeurosis; part of this aponeurosis attaches to the semicircular ligament. The *rectus ventralis* 4, like that in the other species, inserts onto hypobranchial 3 entirely via the semicircular ligament.

Since in *Cichla* the arrangement of these muscles and their insertions are like those in *Serranus*, it would seem that the presence in other cichlids of a semicircular ligament should be considered a derived condition. That interpretation is complicated, at least for the moment, by the presence in *Perca fluviatilis* of a semicircular ligament and muscle insertions exactly like those in cichlids.

A semicircular ligament is present in the pomacentrid *Abudefduf leucozona*, in the labrid *Centrolabrus trutta* and in the embiotocid *Cymatogaster aggregata*. In these taxa, however, there are differing types of muscle association with the ligament, none of which is represented in the cichlids examined. For example, in the pomacentrid and the labrid only *rectus ventralis* 4 inserts on the semicircular ligament, whilst in the embiotocid, although some part of both it and *obliquus ventralis* 3 insert in that way, the overall arrangement of the ventral gill-arch musculature differs greatly from that in the cichlids, pomacentrids and labrids.

Clearly, a lot more comparative data derived from cichlids and from percoid outgroups are needed before the transformational polarity of these various conditions can be established. It is possible, for example that the *Cichla-Crenicichla* situation is not, as it now seems, the plesiomorphic one. It might be a secondary reversion to the 'primitive' state and hence can be treated as a derived feature.

Buccopharyngeal and swimbladder anatomy

No hanging pad (see Trewavas, 1974: 389–391; Greenwood, 1983: 265–267) of the type found in *Chromidotilapia* is present in any of the *Hemichromis* species examined. As in most African cichlids, however, the pharyngeal epithelium immediately anterior and somewhat lateral to the upper pharyngeal bones is noticeably thickened. In at least some *Hemichromis* the thickening is

more pronounced than is usual in most other African cichlids, and the region could be described as having the appearance of an incipient hanging pad. Unfortunately, this region of the pharynx is easily affected by preservation and by the immediate post-mortem history of the specimen, especially temporary dehydration; a once substantially pachydermatous pad can be much reduced in size. Similar factors may also affect the degree to which a sulcus is apparent between the pad-like region and the less thickened tissues of the posterior buccal roof.

A deep sulcus, like that in *Chromidotilapia*, is present in *Hemichromis fasciatus*, but is either absent or represented by a faint transverse depression in specimens of *H. bimaculatus*, *H. letourneauxi*, *H. lifalili* and *H. paynei* examined. When a deep sulcus is present it is interrupted in the midline so that, effectively, there are distinct left and right sulci.

The frenum connecting the suspensorium with the first gill-arch inserts high on that arch, well above the epi-ceratobranchial articulation (see Trewavas, 1973: 18; 1974:391). This is apparently the common condition in African cichlids, although not in (?all) tilapiines (see Trewavas, 1973:18).

The thin-walled swimbladder in *Hemichromis fasciatus* is bilobed anteriorly from a point level with the posterior margin of the third centrum. Each lobe extends anteriorly to about the posterior margin of the second vertebra, and touches the Baudelot's ligament of its side. There is no posterior extension of the swimbladder beyond the limits of the visceral cavity. The transverse septum, which has a moderately large foramen ventrally, lies somewhat posteriorly in the bladder at a point about level with the pleural rib sixth from the end of the series.

Little has been published on swimbladder anatomy and morphology in cichlids (see Cichocki, 1976:115-116), but from personal observations the *Hemichromis* swimbladder would seem to be in no way unusual.

The phylogenetic status of *HEMICHROMIS*

The ultimate object of this paper was to review, in the light of new anatomical data, two questions. First, is *Hemichromis*, as Cichocki (1976:184) and Van Couvering (1982:fig. 11) have indicated explicitly, and others have suggested, a primitive African cichlid? Second: can one identify the sister-group for *Hemichromis*?

That *Hemichromis* is a substrate brooder (see Loisel, 1979 for further details and references) would, perforce, give it a primitive status relative to any mouth-brooding taxon with which it shared a common ancestry. But, apart from its reproductive characteristics (which are rarely mentioned by authors who would rank *Hemichromis* as primitive) it is difficult to determine from previous accounts just why the taxon has been given its rating as a primitive African cichlid.

Neither Pellegrin (1903), Sauvage (1910), nor Regan (1922) undertook any detailed study of *Hemichromis* anatomy, and even Cichocki's (1976) opinion is weakened by his having only compared it with three other African genera. Van Couvering's (1982) work, too, is limited by the few cichlid out-groups she examined and by the few anatomical features which were taken into account. Finally, and most important, none of these authors clearly indicates their reasons for assigning *Hemichromis* to its plesiomorphic status within the family.

Assessing the various anatomical features discussed earlier, both in relation to other African cichlids and to those from the Neotropics, Asia and Madagascar, *Hemichromis* is seen to exhibit two clear-cut autapomorphies, namely the nature of the ethmopalatine articulation, and the development of a hyomandibulad pit. The absence of lateral ethmopalatine ligaments might be considered a third apomorphy, but this character could be correlated with the unusual ethmopalatine joint system in *Hemichromis*.

Besides its autapomorphic characters, *Hemichromis* has derived features which are shared with many other members of the family. For example, the cranial apophysis for the upper pharyngeal bones is structurally of the *Haplochromis* type, a character shared with numerous other African taxa but only one Neotropical species, *Cichla* (see Greenwood, 1978 for discussion of this feature). When compared with Neotropical species, *Hemichromis*, like other African taxa shows

the derived condition of the *adductor arcus palatini* muscle extending onto the palatine bone (p. 156). In the gill-arch musculature, the association of the *obliquus ventralis* 3 and *rectus ventralis* 4 muscles with a semicircular ligament (p. 163) is a derived condition shared with a great number of African and Neotropical cichlids, and also with the single Madagascan species in which the muscles could be checked. The absence of a calyx (p. 145) is apparently a derived feature, and one which *Hemichromis* shares with some Neotropical taxa but with no other African species; it is very doubtful, however, if this feature can be treated as a true synapomorphy. The absence of a laterosensory canal through the anguloarticular bone is seemingly the only synapomorphic feature in *Hemichromis* having a very restricted occurrence outside the genus, otherwise being found only in '*Pelmatochromis*' *thomasi*. There are other features in *Hemichromis*, such as the glandular pseudobranch, the single coronal lateralis canal opening, edentulous vomer, and the single predorsal bone, which are very widely shared with other African and Neotropical taxa, and are represented in the plesiomorphic state only amongst the etropline cichlids of Madagascar and Asia.

The sum of these autapomorphic and synapomorphic features in *Hemichromis* is notable. What then of its plesiomorphic or supposedly plesiomorphic characters?

A derived character probably synapomorphic for African cichlids is the presence of an anteroventral palatomaxillary ligament (see p. 158; also Cichocki, 1976). This ligament is absent in *Hemichromis*, but that could be correlated with the peculiar ethmopalatine articulation in the genus; if that is so, then it cannot be ranked as a plesiomorphic feature for *Hemichromis*. The very slight extent to which, in *Hemichromis*, the *levator posterior* muscle of the dorsal gill-arches is associated with the horn of the lower pharyngeal bone (see p. 160), and the retention of some contact between the fourth *levator externus* muscle and the fourth epibranchial bone, are both plesiomorphic features. However, a similar situation obtains in several of the African taxa I examined (and also in *Cichla* [Stiassny, 1982; pers. obs.]). The lack of a discrete shank spine on epibranchial 4, and the shape of that bone's quadrangular region (see p. 151), are, however, plesiomorphic features neither of which is so clearly exhibited in any other African taxon, even those in which the condition of *levator externus* 4 and the *levator posterior* muscles is comparable with that in *Hemichromis*.

The presence in *Hemichromis* of a definite articulation between the metapterygoid and the anterior flange of the hyomandibula is a plesiomorphy, but its expression here is less primitive than that of a sutural union between these bones, as is found in some Neotropical taxa (see p. 145). The absence of a calyx in *Hemichromis*, however, may well be an autapomorphy, one not recorded in any other African cichlid, but one which is known from some Neotropical species (see p. 146).

The occurrence of only four openings to the lateralis system in the lachrymal (p. 147) is another plesiomorphic feature (Cichocki, 1976; Trewavas, 1983:9; see also Greenwood, 1983) and one found in all Neotropical species as well as in *Eetroplus* (Asia) *Paretroplus* and *Paratilapia* (both Madagascan). In African cichlids, four openings are present only in *Pseudocrenilabrus*, *Nanochromis*, *Pelmatochromis*, *Pterochromis*, *Thysia* and some *Pelvicachromis* species, as well as in certain *Oreochromis* species (Trewavas, 1983:9; pers. observations). Trewavas (*op. cit.*), however, considers that the condition in the *Oreochromis* species represents a secondarily derived state evolved from the usual five openings which characterize the great majority of African taxa.

Total vertebral counts in *Hemichromis* (25–28, mode 25), and the relative number of abdominal and caudal vertebrae (12–15 and 11–14 respectively), fall within the range considered as plesiomorphic for cichlids (see Stiassny, 1982:449). Again, similar counts and ratios are found in other African and in Neotropical species, although the figures for *Hemichromis* are in the lower and thus presumably least derived part of that range.

Zihler (1982:564) identifies the coiling pattern of the gut in *Hemichromis fasciatus* and *H. bimaculatus* as '... generalized or primordial', and of a type not found in any of the several other African species he studied, although it does occur in some Neotropical cichlids. Unfortunately, Zihler's review takes account of only one etropline genus (*Eetroplus*) and does not include *Pelmatochromis*, *Thysia*, *Nanochromis*, *Pterochromis* or *Pseudocrenilabrus*, taxa which, for various reasons are thought to be 'primitive' members of the African cichlid radiation. Despite

that limitation, however, Zihler's work clearly establishes that gut morphology in *Hemichromis* cannot be considered of a derived type.

Fin-ray counts and the nature of the underlying skeletal structures, both in the paired and unpaired fins of *Hemichromis* are shared with several taxa, especially African species. These features probably should be ranked as plesiomorphies, although a detailed analysis of their status has yet to be made. Whether or not the small process on the second postcleithrum in *Hemichromis* can be considered a plesiomorphy is also indeterminable (see p. 154).

In summary it would seem that the majority of plesiomorphic characters in *Hemichromis* are widely symplesiomorphic in cichlid fishes, and that none can be used to categorize *Hemichromis* as an especially 'primitive' taxon within the family. Granted its reproductive biology (see p. 164) must place it amongst the less derived members of the family. But within these substrate brooding species (which, as a group, cannot on that basis, be taken to have any phyletic coherence) *Hemichromis* does not exhibit an especially high number of plesiomorphic traits. In contrast, it would appear to have a greater number of autapomorphic features than do the other African substrate brooders.

At least for the moment there would seem to be no grounds for ranking *Hemichromis* as the most primitive living non-tilapiine cichlid taxon in Africa, as was recently implied by Van Couvering (1982). Even Cichocki's (1976:184) assessment that 'The primitive position estimated for *Hemichromis* is in complete accord with the assessment of Pellegrin . . .' would seem to be somewhat over emphatic, although valid with respect to its spawning habits. But then, there are other substrate brooders amongst the non-tilapiine African cichlids, and none of those has as many derived features as does *Hemichromis*.

The problem of recognizing a sister group for *Hemichromis* is complicated by the genus exhibiting what, in that context, are a predominance of autapomorphies and symplesiomorphies, a difficulty frequently faced by those who work on cichlid fishes. There are, of course, several synapomorphic features, but these are so widely shared as to be useless except in recognizing sister-groups at the highest hierarchical levels. Synapomorphic features of a more circumscribed kind are difficult to identify.

One outstanding autapomorphy for *Hemichromis* lies in the precise nature of its ethmopalatine articulation. Basically, however, the articulation can be classified in one of the two major articulation types found in the Cichlidae. That is, a single rather than a double contact between the palatine and the ethmoid complex.

The majority of African cichlids have a double articulation (pp. 131–132), the palatine contacting the lateral face of the lateral ethmoid anteriorly near or on its suture with the vomer, and posteriorly with a ventrally directed, drum-like facet on the lateral ethmoid near that bone's median margin (see p. 139). Judging from outgroup comparisons with other percoids (eg *Serranus*, *Lates* and *Perca*) and with sub-perciform taxa as well, this articulation type must be considered plesiomorphic (see also Cichocki, 1976:73).

In sharp contrast to the African taxa, most Neotropical species have only the anterior palatoethmoid articulation; the posterior laminar process of the palatine (if developed) has no contact with the lateral ethmoid.

If the double articulation is taken to be plesiomorphic, then many Neotropical taxa show the derived condition, as do a few African taxa (including *Hemichromis*). Furthermore, since both the derived single articulation and the plesiomorphic double one occur in Neotropical and African cichlids, and both occur in the Madagascan taxa, it could be argued that the existence of the two types indicates an early dichotomy in the phylogenetic history of the family.

Unfortunately for that hypothesis there is a suggestion that the derived single articulation may have evolved more than once within the Cichlidae. Evidence for that possibility stems chiefly from the occurrence of both types within the African genus *Bathybates* of Lake Tanganyika. Three *Bathybates* species have a single articulation, two have the typical double type, and one species, *B. ferox*, has both types, with the double joint occurring more frequently than the single one.

This possibility of repeated and independent evolution is reinforced by the occurrence of the single articulation type in one species of *Sarotherodon*, *S. linelli*, a member of a tilapiine genus in

which otherwise only the double articulation is present. Intriguingly, and perhaps significantly for the thesis of independent evolution, *Sarotherodon caroli*, an apparently close relative of *S. linelli* (Trewavas *et al.*, 1972:52) living sympatrically with it in the isolated Cameroonian crater lake Barombi Mbo, has a double articulation.

Thus, on the basis of current information, I do not think one can safely interpret the *Hemichromis* ethmopalatine articulation as indicative of the genus being more closely related to taxa with a single articulation than to those with the double type.

Regan's (1922) implied close relationship of *Hemichromis* and *Haplochromis* apparently was based solely on the two taxa having a *Haplochromis*-type of neurocranial apophysis, and was influenced by his belief in the character as an important indicator of phylogenetic relationship (see discussion in Greenwood, 1978). There are no other synapomorphies shared only by *Hemichromis* and *Haplochromis* (the latter broadly conceived as it was by Regan; see Greenwood, 1979). Neither are there any synapomorphies shared only with particular members of the broader but non-phylogenetic haplochromine concept currently used to embrace those African cichlids with a *Haplochromis*-type of apophysis (see Greenwood, 1978; 1979). Furthermore, it would seem inadvisable to consider the possession of a *Haplochromis*-type apophysis as indicative of close phyletic relationship (Greenwood, 1978). In itself, an apophysis of that type can be considered derived relative to the *Tilapia*-type, but a *Haplochromis* apophysial type could have evolved, independently, on more than one occasion; relevant ontogenetic information is contained in Ismail *et al.*, 1982.

Hemichromis, it will be recalled, has been considered a close relative of the extinct African genus *Palaeochromis* (Sauvage, 1907, 1910). The grounds for that alliance, namely body-form, vertebral counts and oral tooth morphology, cannot be treated as critical in a phylogenetic context. Body form can be considered only a matter of overall similarity, and in this particular instance a similarity repeated many times over in different lineages; the vertebral counts in both genera are plesiomorphic features, and the supposed similarity in oral dentition can be discounted by Van Couvering's recent examination of the two genera (Van Couvering, 1982:93). Sauvage (1910:52) also believed that *Palaeochromis* linked *Hemichromis* with the Neotropical genus *Acara* (a relationship for *Hemichromis* first postulated by Pellegrin, 1903); in this context, *Acara* should probably be read as *Aequidens*. Like Pellegrin, Sauvage gave no reasons for his suppositions, and the proposal must also have been made on the basis of overall similarity. I can find no synapomorphies suggesting even a moderately distant relationship between either *Hemichromis* and *Palaeochromis* or *Hemichromis* and any Neotropical taxon.

Recently, Loiselle & Welcomme (1972:53 *et seq.*), when considering the relationship of their new West African genus *Thysia*, thought (*op. cit.*:57) it reasonable to consider *Thysia* '... as a rather generalized cichlid most closely allied to the *Hemichromis bimaculatus*-*Pelmatochromis thomasi* group within *Hemichromis sensu lato*'. They go on to comment that '... These two groups, together with the *Hemichromis fasciatus* species group within *Hemichromis*, can be considered an oligophyletic assemblage comparable to *Tilapia sensu lato*. A comparable arrangement seems applicable to the *Nanochromis-Pelvicachromis-Chromidotilapia* group of cichlids which, on the basis of evidence presented in Thys (1968a), represent a common evolutionary assemblage. We therefore propose two further groups of cichlids, the hemichromine cichlids, consisting of *Hemichromis sensu lato* and *Thysia*, and the pelmatochromine cichlids consisting of the genera *Nanochromis*, *Pelvicachromis* and *Chromidotilapia*'.

There are several apparently phylogenetic statements made in those quotations, but none would seem to stand up to closer examination.

Loiselle and Welcomme's association of *Hemichromis* with *Thysia* is not based on any synapomorphic characters (see Loiselle & Welcomme, 1972:53-54; and compare with pages 164-165 above). Once again 'affinities' were based on symplesiomorphies, including spawning habits. In this instance, the number of listed similarities between *Hemichromis* and *Thysia* are outnumbered by their dissimilarities (Loiselle & Welcomme, 1972:56), thus making it difficult to understand, without further justification, why Loiselle and Welcomme concluded that the two genera were 'closely allied' or why the two taxa should form a distinct subgroup within the African assemblage.

The suggestion that '*Pelmatochromis*' *thomasi* might be closely related to *Hemichromis* (see quote above) was initiated by Thys van den Audenaerde (1968:382), mainly on the grounds of its coloration and reproductive behaviour being much like that in *H. bimaculatus* (*sensu lato* in the light of Loiselle's [1979] later revision of *Hemichromis*).

'*Pelmatochromis*' *thomasi* has a typical double ethmo-palatine articulation (see p. 139), lacks a ventral vomerine support for the palatine, has both lateral and anteroventral palato-ethmoidal ligaments, and lacks a hyomandibular pit. In other words, it shares none of the principal apomorphies characterizing *Hemichromis*. However, it does share one derived feature with that genus, namely the absence of a latero-sensory canal running through the anguloarticular, a presumed apomorphy not recorded in any other cichlid. On that feature, and that feature alone, '*Pelmatochromis*' *thomasi* would appear to be the most likely candidate for consideration as the sister taxon to *Hemichromis*.

The use of a 'loss' character as a synapomorphy must be treated with considerable circumspection, especially when, as in this case, it is not backed by other synapomorphies. Thus, even though there are no contraindicative characters, this postulated sister-group relationship should be considered as a very tentative hypothesis. The possibility that it might be corroborated by ethological evidence (see Thys van den Audenaerde, 1968) requires further investigation but would be well worth pursuing. At present there are insufficient data to establish the polarity of such features; the fact that '*P.*' *thomasi* and the *Hemichromis* species are substrate brooders is of no value in establishing relationships since that is a plesiomorphic character.

Although I have used the binomen '*Pelmatochromis*' *thomasi*, the generic relationships of the species are currently *incertae sedis*. Trewavas (1973:14) specifically excludes *thomasi* from *Pelmatochromis*. On the basis of those characters she used to redefine the genus I would agree with its exclusion, and likewise cannot include the species in either *Pelvicachromis* or *Chromidotilapia*, the other elements of the earlier *Pelmatochromis* generic concept. Rather than confuse the issue further by creating a new genus for *thomasi*, and pending a phylogenetically orientated revision of *Pelmatochromis*, *Pelvicachromis* and *Chromidotilapia*, I chose to refer to the species as '*Pelmatochromis*' *thomasi*. In that way both its uncertain generic position and its overall superficial phenetic 'relationships' can be indicated.

If '*Pelmatochromis*' *thomasi* and *Hemichromis* are sister taxa, the question then arises of their relationship to other African groups. For the moment there are few anatomical or morphological data indicating where that relationship might lie. One character, which might provide an escape from that dilemma, but only after much more research, concerns the nature of circulus patterns on the scales of *Hemichromis*. Trewavas (1973:14; fig. 10) drew attention to the peculiar 'gothic arch' pattern of the central circuli in the posterior field of the body scales in *Hemichromis* and '*Pelmatochromis*' *thomasi*, and the presence of a similar pattern on at least some scales in other West African taxa, viz: *Tilapia ruweti*, *Pelmatochromis buettikoferi*, *P. ocellifer*, *P. nigrofasciatus* and young specimens of *Pterochromis congicus*. Unfortunately, little is known about the finer morphology of the scales in most cichlid fishes, and the primitive or derived status of the 'gothic arch' pattern is undetermined. A preliminary survey of Neotropical and African species in the BMNH collections indicates that the pattern occurs in 10 of the 116 Neotropical species examined (sometimes in one but not all species of a genus), that it is absent in all but three African tilapiine species, and that it occurs in some non-cichlid taxa as well (e.g. *Serranus cabrilla*).

From those data I would be chary of using the 'gothic arch' pattern alone to suggest relationships between the African species in which it occurs, the more so since, except for *Hemichromis* and '*Pelmatochromis*' *thomasi*, there are no congruent synapomorphies known to be shared only by those taxa.

Parenthetically, it is interesting to record that Thys van den Audenaerde (1968), expressed doubts about the congeneric status of *H. fasciatus* and *H. bimaculatus*, mainly because the latter has much smaller canine-like teeth in its oral dentition. Although, because of their various uniquely shared specializations, it would be difficult to doubt the close relationship of the two species, there are other features, especially vertebral numbers (p. 155) and the shape of the premaxilla (p. 148) which suggest the possibility of a *fasciatus-bimaculatus* lineage dichotomy

within the genus. Thys van den Audenaerde (1968:372) also treated the species *cerasogaster* Boulenger, 1898 as a member of the genus *Pelmatochromis*. My anatomical studies would, however, fully confirm Loisel's (1979:88) inclusion of that species in *Hemichromis*.

In the latter paper Loisel (*op. cit.*: 94) develops further the idea, first aired by Loisel & Welcomme (1972), of a close relationship between *Thysia* and *Hemichromis*. He argues for relationship on the grounds that *H. cerasogaster* has the most plesiomorphic, that is multi-seriate, dental pattern of all *Hemichromis* species, and that in this feature there is a close resemblance between it and *Thysia*. Since, quite explicitly, this proposal is based on a symplesiomorphy it adds nothing to the other arguments, also based on symplesiomorphies, which were put forward earlier by Loisel & Welcomme (1972).

Finally, mention must be made of the most recent view on a possible African sister-group relationship for *Hemichromis*, albeit one on a taxonomically broader scale than any put forward previously. This is expressed in Van Couvering's cladogram of African (and Madagascan) cichlid relationships (Van Couvering, 1982:fig. 11). Here, but without any detailed reasoning given in the text, or synapomorphies included in the cladogram, *Hemichromis* is shown as the sister group of a *Pseudocrenilabrus* plus a *Haplochromis* lineage. *Haplochromis* in this context is apparently taken to include all those African taxa which Regan (1920; 1922 and later papers; see Greenwood, 1978) had described as having a *Haplochromis*-type of pharyngeal apophysis (see Van Couvering, 1982:17). *Pseudocrenilabrus*, however, is restricted to that genus alone. Again, I can find no synapomorphies to corroborate Van Couvering's grouping, and she offers none herself.

Apart from Pellegrin's (1903) and Sauvage's (1910) suggestion of close resemblance between *Hemichromis* and *Acara*, there have been no published indications of a possible relationship between *Hemichromis* and any Neotropical genus or generic group.

To the best of my knowledge, the monophyly of the Neotropical cichlids has not been established. Nor, for that matter has the monophyly of the African taxa been established either. However, Cichocki (1976:74) noted in the few African taxa he studied, but not in any of the Neotropical or Madagascan species, that the *adductor arcus palatini* muscle extends forward to insert on the palatine as well as on the pterygoid bones. I can now confirm that there is an anterior extension of this muscle in all the African taxa I examined (see p. 156). Since the muscle does not extend forward in any of the outgroup taxa examined by Cichocki or myself, there is a strong possibility that it is not only a derived feature but a synapomorphy indicating a monophyletic origin for the African species.

If that is so, then *Hemichromis* ultimately shares a common ancestry with all other African species (The Neotropical *Cichla*, despite its *Haplochromis*-type pharyngeal apophysis [see Regan, 1920], is excluded). Certainly, when other apomorphic features are taken into account, *Hemichromis* shows no close relationship with any Neotropical taxon, despite the fact that a single and anterior ethmopalatine articulation is commoner amongst Neotropical than it is amongst African taxa (see p. 139). The similarities which do exist between *Hemichromis* and the Neotropical cichlids (eg. breeding behaviour, isomorphic or weak sexually dimorphic coloration, four-pored lachrymal bone, morphology of the fourth epibranchial bone) are all symplesiomorphies.

To summarize, it would seem that, apart from '*Pelmatochromis*' *thomasi*, none of the previously suggested sister-group relationships for *Hemichromis* meet the requirements necessary to establish, unequivocally, the taxon's phyletic rather than its superficial phenetic affinities. The previously suggested relationship of *Hemichromis* with '*Pelmatochromis*' *thomasi* was based on features whose phyletic value cannot be assessed (*ie* coloration and breeding behaviour). The current suggestion is based on a single synapomorphy, and a 'loss' feature at that (albeit one which, seemingly has not been lost in any other cichlid, and which is rarely absent in other percoids).

Conclusion

On the evidence currently available, *Hemichromis* would seem to be a fairly isolated lineage within the radiation of African cichlids, of which it is phylogenetically a part. The lineage is

recognizable on the basis of at least two autapomorphic features. Its sister group, with which it shares a single synapomorphy, is the taxon '*Pelmatochromis*' *thomasi*, a species whose generic placement is at present undecided.

Hemichromis exhibits several primitive features which, although retained in many Neotropical taxa, are lost in the great majority of African species. It does, however, share one derived feature with, if not all, then at least the majority of African taxa, and shows none which might suggest a closer relationship with the Neotropical rather than with the African taxa.

Although *Hemichromis* must, on several features, be ranked with primitive African members of the family it cannot be considered the most primitive member of that subgroup. The relationships of *Hemichromis* (+ '*Pelmatochromis*' *thomasi*) amongst the more primitive African cichlids are still undetermined.

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References

- Aerts, P. 1982. Development of the musculus levator externus IV and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Teleostei: Cichlidae). A discussion on the shift hypothesis. *J. Morph.* **173**: 225–235.
- Anker, G. Ch. 1978. The morphology of the head muscles of a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **28**: 234–271.
- Barel, C. D. N., Witte, F. & van Oijen, M. J. P. 1976. The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas, 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **26**: 163–265.
- Boulenger, G. A. 1901. *Les poissons du bassin du Congo*. Publ. État. indep. Congo. Bruxelles.
- Cichocki, F. 1976. *Cladistic history of cichlid fishes and reproductive strategies of the American genera*. Ph.D. thesis, University of Michigan, Ann Arbor.
- Goedel, W. 1974. Beiträge zur vergleichenden und funktionellen Anatomie des Kopfes von *Tilapia* (Cichlidae: Teleostei). *Zool. Jb. (Anat.)* **92**: 220–274, 321–383.
- Greenwood, P. H. 1978. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. *Bull. Br. Mus. nat. Hist. (Zool.)* **33**: 297–323.
- 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. *Bull. Br. Mus. nat. Hist. (Zool.)* **35**: 265–322.
- 1983. The *Ophthalmotilapia* assemblage of cichlid fishes reconsidered. *Bull. Br. Mus. nat. Hist. (Zool.)* **44**: 249–290.
- 1984. The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers. *Bull. Br. Mus. nat. Hist. (Zool.)* **47** (4): 187–239.
- Ismail, M. H., Verraes, W. & Huysseune, A. 1982. Developmental aspects of the pharyngeal jaws in *Astatotilapia elegans* (Trewavas, 1933) (Teleostei: Cichlidae). *Neth. J. Zool.* **32**: 513–543.
- Johnson, G. D. 1980. The limits and relationships of the Lutjanidae and associated families. *Bull. Scripps Instn. Oceanogr.* **24**: 1–114.
- Kaufman, L. S. & Liem, K. F. 1982. Fishes of the suborder Labroidae (Pisces: Perciformes): Phylogeny, ecology and evolutionary significance. *Breviora* no. 472: 1–19.
- Liem, K. F. & Greenwood, P. H. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. *Am. Zool.* **21**: 83–101.
- & Osse, J. W. M. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. *Am. Zool.* **15**: 427–454.

- Loiselle, P. V.** 1979. A revision of the genus *Hemichromis* Peters 1858. *Annl. Mus. r. Afriq. Cent.* ser. 8vo. Zool. no. 228: 1–124.
- & **Welcomme, R. L.** 1972. Description of a new genus of cichlid fish from West Africa. *Revue Zool. Bot. afr.* **85**: 37–58.
- Pellegrin, J.** 1903. Contribution a l'étude anatomique biologique et taxonomique des poissons de la famille des cichlidés. *Mem. Soc. zool. Fr.* **16**: 41–402.
- Regan, C. T.** 1920. The classification of fishes of the family Cichlidae-I. The Tanganyika genera. *Ann. Mag. nat. Hist.* (9) **5**: 33–53.
- 1922. The classification of the fishes of the family Cichlidae.—II. On African and Syrian genera not restricted to the Great Lakes. *Ann. Mag. nat. Hist.* (9) **10**: 249–264.
- Sauvage, H. E.** 1907. Sur des poissons de la famille des Cichlides trouvés dans les terrain tertiaire de Guelma. *C. r. hebd. Séanc. Acad. Sci. Paris*, **145**: 360–361.
- 1910. Les poissons des marnes sulfogypseuses de la vallée de la Seybouse. *Matériaux carte géol. d'Algérie: Paléontologie*, Ser. 1 **4**: 50–54.
- Stiassny, M. L. J.** 1981a. Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika. *Bull. Br. Mus. nat. Hist.* (Zool.) **40**: 67–101.
- 1981b. The phyletic status of the family Cichlidae (Pisces, Perciformes): A comparative anatomical investigation. *Neth. J. Zool.* **31**: 275–314.
- 1982. The relationships of the neotropical genus *Cichla* (Perciformes, Cichlidae): a phyletic analysis including some functional considerations. *J. Zool. Lond.* **197**: 427–453.
- Thys van den Audenaerde, D. F. E.** 1968. A preliminary contribution to a systematic revision of the genus *Pelmatochromis* Hubrecht sensu lato (Pisces, Cichlidae). *Revue Zool. Bot. afr.* **77**: 349–391.
- Trewavas, E.** 1973. I. On the cichlid fishes of the genus *Pelmatochromis* with proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. *Bull. Br. Mus. nat. Hist.* (Zool.) **25**: 1–26.
- 1974. The freshwater fishes of rivers Mungo and Meme and Lakes Kotto, Mboandong and Soden, west Cameroon. *Bull. Br. Mus. nat. Hist.* (Zool.) **26**: 329–419.
- 1983. *Tilapiine fishes of the genera Sarotherodon, Oreochromis and Danakilia*. British Museum (Nat. Hist.), London.
- **Green, J. & Corbet, S. A.** 1972. Ecological studies on crater lakes in west Cameroon. Fishes of Barombi Mbo. *J. Zool. Lond.* **167**: 41–95.
- Van Couvering, J. A. H.** 1982. Fossil cichlid fish of Africa. *Spec. pap. Paleon. Assn.* no. 29: 1–103.
- Vandewalle, P.** 1971. Comparaison ostéologique et myologique de cinq Cichlidae africains et sud-américains. *Annl. Soc. r. zool. Belg.* **10**: 259–292.
- 1973. Osteologie caudale des Cichlidae (Pisces, Teleostei). *Bull. Biol. Fr. Belge.* **107**: 275–289.
- Zihler, F.** 1982. Gross morphology and configuration of digestive tracts of Cichlidae (Teleostei, Perciformes); Phylogenetic and functional significance. *Neth. J. Zool.* **32**: 544–571.